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Evaluating competition, interactions and trait differences between vulnerable marine ecosystem taxa in climate changing ocean: laboratory studies on flow and feeding responses by gorgonians (Condor Seamount) and cold-water scleractinian corals, sponges and bivalves (Norwegian Shelf).

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Declaration

I certify that this thesis has been composed solely by myself and that it has not been submitted, in whole or in part, in any previous application for a degree. Except where it states otherwise by reference or acknowledgment, the work presented is entirely my own.

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Stephanie Liefmann Castellanos

Edinburgh October 2020

Abstract

Cold-water corals reefs, gardens and sponge grounds are vulnerable marine ecosystems (VMEs) as defined by UN resolution 61/105. These VMEs are protected from destructive fishing practices and are recognised due to the biodiversity they support. However, despite such international policy imperatives, we lack even basic understanding of ecological interactions between VME indicator taxa. For example, we do not understand how co-occurring VME indicator species interact or compete with each other under different conditions, such as water flow and food concentrations, both of which are likely to change in direct response to climate change. This thesis aimed to evaluate competition and trait differences underlying VME indicator species.

Taxa co-occurring in 2 different VMEs were tested under laboratory conditions. From the Condor Seamount (Azores archipelago) the octocorals *Viminella flagellum* and *Dentomuricea meteor*, were compared according to two traits: skeletal composition and sclerite shape and size. *Viminella flagellum* and *D. meteor* were also tested for competition interactions under 2 different flow regimes. From the Norwegian continental shelf, feeding efficiency, particle size and type preference under varying flow and natural food conditions was measured for species with different feeding strategies/traits (active and passive suspension feeders). The tested species include a scleractinian coral (*Lophelia pertusa*), demosponges *(Geodia barretti, Phakellia ventilabrum* and *Stryphnus* sp.) and a bivalve (*Acesta excavata*). The different traits found in co-occurring species

can represent different strategies permitting them to exploit and withstand the variable a-biotic and food supply conditions, meaning they can niche partition.

Differences in feeding efficiency are more evident when comparing across taxa than individual species, reinforcing that trait differences are crucial and should be taken into consideration. Trends suggest that different species have preferences for different subsets of the natural occurring seston, which could be mediated by the different traits. Understanding the preferences of different species, and relating them to the predicted changes in food composition availability and flow changes will help refine future species distribution models and ecosystem functioning of VMEs in a changing ocean. Evidence highlights how exclusive competition could occur under specific conditions between the study species. The findings suggest other interactions besides competition should be taken into account when studying coexisting species, for example facilitating cascades and nutrient recycling. Species interactions should be taken into account when performing species distribution models in order to better predict the effect of changing conditions in ecosystem functioning.

Lay summary

Coral reefs and sponge aggregations are considered one of most diverse, colourful, productive, and beautiful landscapes on Earth, but they are usually associated with tropical warm waters. However, deep-sea floor harbours a vast amount of species just like the shallow tropics. Because of their remoteness, these natural assemblages have not been as extensively studied as shallow coral reefs. Nevertheless, they are very important for the functioning of our oceans, and are the focus of management strategies such as vulnerable marine ecosystems designation.

Deep-sea corals and sponges do not have symbiotic algae in their tissue for photosynthetically derived carbon, and instead are dependent on the food passively or actively caught from the water column, meaning food can be a limiting resource. Several deep-sea corals, sponges and other species co-occur and form vulnerable marine ecosystems. The interactions and relationships of these different species are poorly characterised. These interactions are important to understand the functioning of deep-sea ecosystems and how it could change due to projected changes in environmental stressors. Interactions can be influenced by the different characteristics of the species. This thesis aimed to 1) evaluate how certain characteristics relate to the conditions the species live in, and 2) to assess the interactions between different species and whether they compete. The results of this thesis did not show evidence of competition, but underlined how species can co-exist, likely because they exploit different resources and conditions. Changing conditions such as flow and food availability have the possibility to affect

the interactions between the different species composing the ecosystems. Understanding these interactions could be pivotal to understand how ecosystem functioning and services could be affected by global change.

Aknowledgements

First and foremost I have to thank God, with him everything is possible.

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Contents

List of abbreviations

AMOC: Atlantic meridional overturning circulation

AW:Ash weight

AFDW: Ash free dry weight

ARQDAÇO monitoring programme, University of the Azores

ED-X: Energy Disperssive X-ray

CR: Clerance Rate

CWC: Cold Water Coral

DISCOL: Disturbance and Recolonisation experiment

DMS: Degrees Minutes Seconds

DOM: Dissolved Organic Matter

DOP:Departement of Oceanography and Fisheries Portugal

DW:Dry weight

FAO: Food and Agriculture Organization

FITC: Fluorescein Isothiocyanate

FSC: Forward Scatter

HMA: High Microbial Abundance sponges

ICES: International Council for Exploration of the Sea

IMAR: Institute of Marine Research Azores

IMR: Institute of Marine Research Norway

IPCC: Intergovernmental Panel on Climate Change

EA-IRMS: Elemental Analysis Isotope Ratio Mass Analysis

LMA: Low Microbial abundance sponges

NAFO: North Atlantic Fisheries Organisation

NEAFC: North East Atlantic Fisheries Commission

OSPAR: Oslo Paris Agreement

PAMAS: Partikelmess- und Analysesysteme

PerCP: Peridinin-chlorophyll proteins

POC: Particulate Organic Carbon

POM: Particulate Organic Matter

RE: Retention Efficiency

RFMO: Regional Fisheries management Organisations

ROV: Remotely Operated Vehicles

RV: Research Vessel

SEM: Scanning Electron Microscopy

SPM: Suspended Particulate Matter

TOC: Total Organic Carbon

UN: United Nations

UNGA: United Nations General Assembly

VME: Vulnerable Marine Ecosystem

Chapter 1: General introduction

The deep sea is the largest biome on Earth covering at least 65% of the Earth's surface (Sverdrupp et al., 1942), with very little of it explored (Ramirez – Llodra et al., 2011). The deep seafloor encompasses parts of the continental slope and the abyssal plain. Within these slopes and deep basins other geological, and biogenic structures are found, such as mid-ocean ridges, canyons, seamounts, cold-water coral reefs, sponge grounds hydrothermal vents, methane seeps, mud volcanoes, faults and trenches. Amongst these features some of the highest levels of biodiversity on Earth are found (Snelgrove and Smith, 2002; Stuart et al., 2003).

Goods and services from deep-sea ecosystems are also extremely valuable (Armstrong et al., 2012). Some of the assemblages found in the deep-sea form Vulnerable Marine Ecosystems (VME) composed of different taxa, whose interactions we know little about. Interactions between different taxa can influence the relationship between biodiversity and ecosystem functioning (Danovaro et al., 2008). The species forming VMEs have different traits that determine how they interact with each other and their environment (Saito et al., 2020). Better understanding the functionality of VME, will help support policy directives and management strategies to ensure more adequate protection.

The focus of this introduction will be to introduce VMEs, their importance, and the threats they face. It will also summarise key knowledge gaps, such as species interactions, preferences for different food particle sizes and types which will be further explored in the thesis chapters.

1.1. VME definitions

Vulnerable marine ecosystems (VMEs) are groups of species, communities, or habitats that may be vulnerable to impacts from fishing and other anthropogenic activities as defined by the Food and Agriculture Organisation (FAO, 2009). The VME concept started to gain recognition after the United Nations General Assembly (UNGA) 61/105 resolution was passed (UNGA, 2007), and called upon member states to minimise damage to these ecosystems. Resolutions passed by the UNGA are not binding, but the Regional Fisheries Management Organisations (RFMO), which nations are contracting, have the right to adopt legally binding measures.

To be defined as VME, ecosystems have to meet one or more of the following criteria, as dictated by the FAO (2009), and be found in densities predefined by the different RFMOs.

1. Rarity/uniqueness: an area or ecosystem that is unique or that contains rare species whose loss could not be compensated for by similar areas or ecosystems. These include: habitats that contain endemic species; habitats of rare, threatened or endangered species that occur only in discrete areas; or nurseries or discrete feeding, breeding, or spawning areas.
2. Functional significance of the area: discrete areas or habitats that are necessary for the survival, function, spawning/reproduction or recovery of fish stocks, particular life-history stages (e.g. nursery grounds or rearing areas), or of rare, threatened or endangered marine species.

3. Fragility: ecosystems that are highly susceptible to anthropogenic activities.
4. Life history traits of component species that make recovery difficult, such as slow growth rate, late age maturity, low or unpredictable recruitment, and longevity.
5. Structural complexity: An ecosystem that is characterised by complex physical structures created by significant concentrations of biotic and abiotic features.

Several taxa have been acknowledged to be VME indicators because they are the most likely to be found in habitats meeting the criteria for VMEs (NAFO, 2019; NEAFC, 2014), amongst them cold-water corals (CWCs) encompassing reef framework forming and solitary scleractinians, octocoral aggregations (corals gardens) and deep-sea sponge aggregations (NAFO, 2019; NEAFC,2014). Bivalves such as *Neopycnodonte cochlear* are also VME indicator taxa (FAO, 2018; ICES, 2017).

1.2. Types of VMEs

Cold-water corals and sponge grounds form complex biogenic structures on the seafloor and have been known for centuries through bycatch from the fishing industry. In the last few decades, advances in technology have allowed the investigation of the deep sea, and further study of these ecosystems. Cold-water corals are cnidarians and include the stony corals (Scleractinia), soft corals (Octocorallia), black corals (Antipatharia), and hydrocorals (Stylasteridae) (Roberts et al., 2006). Sponge grounds found at comparable depths to CWCs are

mostly composed by Demospongiae and Hexactinnellida (Hogg et al., 2010). Both corals and sponges can form significant structural habitats across a range of depths between 50 to 4000 m in high energy environments that supply food and remove waste products (Freiwald, 2002; Hogg et al., 2010; Roberts et al., 2006). Cold-water coral reefs are composed of reef framework-forming corals, *Lophelia pertusa* and *Madrepora oculata* (Roberts et al., 2009). Dense aggregations of corals are considered coral gardens, dominated by solitary scleractinians, sea pens or octocorals, stylasterids, and/or antipatharians (ICES, 2007). Vulnerable marine ecosystem indicator taxa often co-occur creating mixed VMEs, and can be accompanied by dense aggregations of the bivalve *Acesta excavata* (Figure 1.1).

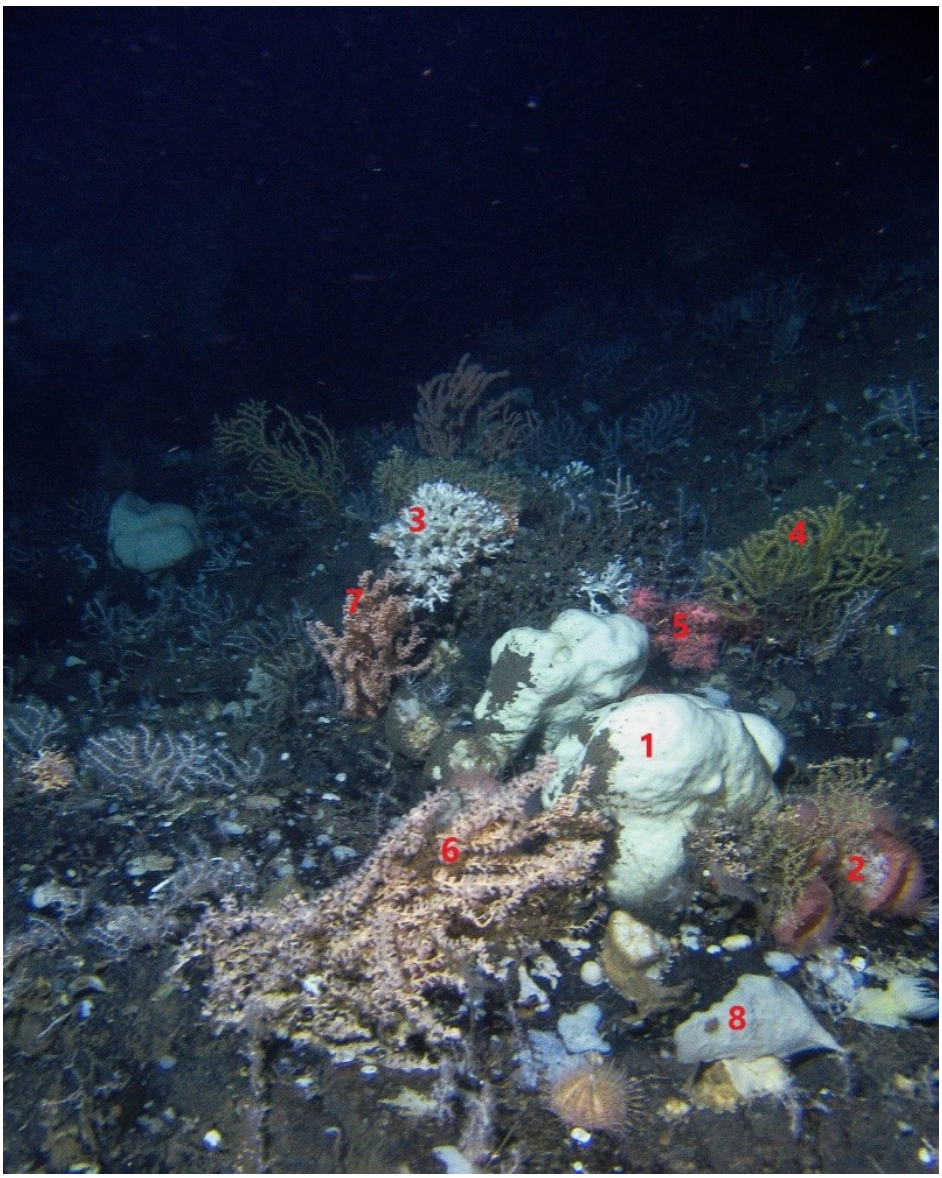

Figure 1.1: Figure showing some of the species diversity found in the Norwegian fjords. 1, *Geodia* sp.; 2, *Acesta excavata*; 3, *Lophelia pertusa*; 4, *Paramuricea placomus*; 5, *Paragorgia arborea*; 6, *Swiftia* sp.; 7, *Primnoa resedaeformis*; 8, *Phakellia* sp. co-occurring on a fjord wall. Photo reproduced from (Järnegren and Kutti, 2014). © Johanna Järnegren

1.3. Importance of VME habitats

The functional significance and structural complexity of CWCs and sponge grounds make them important features of the deep-sea benthic environment. Their structural complexity enables them to be biodiversity hotspots (see below) representing important habitats for the different ontogenetic stages of fish and other taxa. The role in nutrient cycling of these ecosystems also meets the functional significance criteria for VME designation. These concepts will be discussed in more detail below.

1.3.1. Cold-water corals and deep-sea sponges as biodiversity hotspots, meeting the structural complexity, rarity and uniqueness, and functional significance criteria for VME designation

Cold-water corals and deep-sea sponges habitats are important ecosystem engineers in the deep sea, providing structural complexity through their skeletal framework which can harbour a number of associated fauna (Buhl-Mortensen et al., 2010), thus meeting the structural complexity criteria for VME classification. The structures created by cold-water coral reefs, gardens and sponge grounds have been documented to serve as substratum and habitat to support other invertebrates, through elevation for associated organisms to access food, and for protection from physical factors (Buhl-Mortensen et al., 2010). Coral gardens are defined by the OSPAR commission (2010) as a relatively dense aggregation of cold-water corals (CWCs) colonies or individuals of one or more coral species, belonging to different taxonomic groups. Coral gardens may include species from the orders Alcyonacea, Pennatulacea, Antipatharia, Scleractinia and, in some places, Stylasteridae (FAO, 2009; 2016). Coral gardens composed of octocorals also

harbour a number of associated fauna (Buhl-Mortensen and Mortensen, 2005; Carreiro-Silva et al., 2011; Krieger and Wing, 2002).

Fish associations have also been well documented with cold-water benthic habitats in general (Buhl-Mortensen et al., 2010; Husebø et al., 2002; Kutti et al., 2014). Although the nature of these associations has not been completely elucidated, it has been hypothesised that the abundance of fish is linked to habitat complexity which can be created by other structures besides corals (Auster, 2005; Auster et al., 2007). However, more direct evidence of the importance of these habitats for fish has been reported over recent years. For example, Ross and Quattrini (2007) highlighted specific associations between CWC reefs and the following fish species: *Anthias woodsi, Beryx decadactylus, Conger oceanicus,* and *Dysommina rugosa.* Baillon et al. (2012) classified CWCs as fish larvae nurseries. Cat shark (*Galeus melastomus)* eggs have also been found in live *L. pertusa* reefs (Henry et al., 2013) and in gorgonian gardens (Etnoyer and Warrenchuk, 2007). Cold-water corals being used as spawning grounds meets the uniqueness, rarity, and functional significance criteria for VMEs by the FAO. Coral gardens composed of threatened species such as the coral gardens composed of *Funiculina quadrangularis* and *Isidella elongata* also meet the criteria for uniqueness and rarity (Lauria et al., 2017). Coral gardens composed of corals having a restricted distribution, for example *Dentomuricea meteor*, which has been documented only from the Great Meteor and Condor seamounts (Sampaio et al., 2019) meet the rareness and uniqueness criteria. This criterion is more species specific since it

encompasses endemism and threatened species. Equally assessing if the ecosystem in question is not replaceable is site specific and difficult to assess.

Sponge grounds are likewise classified as biodiversity hotspots (Kutti et al., 2013), with higher species richness and abundance of megafauna in sponge grounds compared to non-sponge grounds in the Northwest Atlantic (Beazley et al., 2013; Klitgaard, 1995). The association between fish and sponge grounds is not as clear; in the Træna deep marine protected area in Norway, Kutti et al. (2014) found no correlation between sponge grounds and demersal fish, whereas Kenchington et al. (2013) found that fish biomass and number were negatively correlated with sponge biomass and depth. In the Gulf of Alaska juvenile *Sebastes* sp. were associated with *Aphrocallistes* sp., and no juveniles were observed without sponges (Freese and Wing, 2003). These findings suggest that sponge grounds harbour distinctive fish assemblages, and might be important for certain ontogenetic stages, again reiterating that sponge grounds meet the functional significance, structural complexity, and rareness and uniqueness criteria for VME classification.

The bivalve mollusc *Acesta excavata* was recently discovered to create biotopes and harbour associated fauna (Johnson et al., 2013; Taviani et al., 2019), meeting the structural complexity VME criteria, though this species is not yet recognised as a VME indicator taxa by any of the RFMOs. Several VME locations have already been closed to fishing efforts, or are being managed, in order to protect these ecosystems (Figure 1.2). In order to better understand and classify VMEs and the indicator taxa, more information of their functionality should be

pursued, since the sparse information available might underestimate their functionality and hamper their protection and VME designation. Equally, designation of VME indicator taxa is the responsibility of the different RFMOs, which is based on expert judgement and vary between the different regions possibly depending on the different interpretation given to the FAO criteria (Long et al., 2020; Morato et al., 2018). Despite their importance, these ecosystems are vulnerable to anthropogenic activities as discussed bellow.

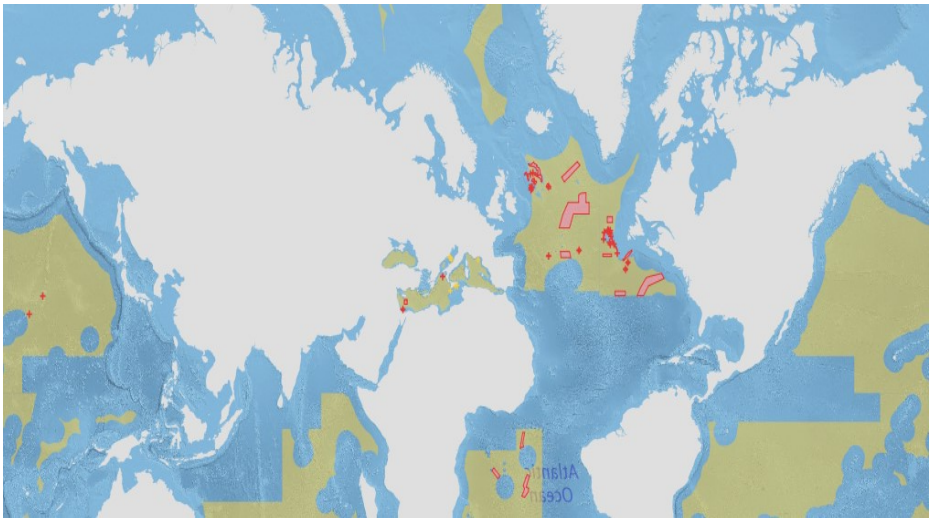

Figure 1.2: World map showing the VME areas beyond national jurisdiction closed to fishing in red and the managed areas in green. Map created using the VME tool from the FAO. For specific coordinated of closure sites in the North Atlantic, the reader is referred to the North East Atlantic Fisheries commission resolution 19:2014 article 11 (NEAFC, 2014), and the North Atlantic fisheries organisation conservation and enforcement measures article 17 (NAFO, 2019)

1.3.2. Threats to VMEs

Various anthropogenic activities threaten the deep sea (Figure 1.3), and have become more prevalent since technology has made it possible to exploit it (Ramirez-Llodra et al., 2011). These threats include fishing, oil and gas exploitations (Table 1.1), which have immediate impacts; climate change, which has insidious medium-long term consequences (Table 1.2), and other exploitative industries that are in the planning face such as deep-sea mining and bioprospecting.

Cold-water corals and sponge grounds have slow recovery rates (Althaus et al., 2009; Buhl-Mortensen et al., 2013; Simon-Lledó et al., 2019) and slow-growth rates (Fallon et al., 2010; Hoffman et al., 2003; Roark et al., 2006; Sherwood et al., 2006; Tracey et al., 2007) making them more susceptible to threats and, hence, meeting the FAO criteria of fragility and life history traits for VME classification.

1.3.2.1. Fishing

Fishing is one of the activities that has had significant impacts to CWCs and sponge grounds, with trawling identified as the most damaging fishing method (Clark et al., 2010; Halpern et al., 2007). The most notable effects of fishing are smoothering (Althaus et al., 2009; Clark et al., 2007;Fosså et al., 2002 Ragnarsson et al., 2017 Hourigan et al., 2007), entangling , intensive long line fishing and gill nets having a significant adverse effect over time (Bergmann and Klages, 2012; Ragnarsson et al., 2017). Excessive sedimentation is also produced by fishing

efforts (Martin et al., 2014) more detail of its effects can be found in Table 1.1. Recovery from fishing endeavours is very slow, 15 years after cessation of fishing activities; seamounts of New Zealand had not shown signs of recovery (Clark et al., 2019).

1.3.2.2. Oil and gas exploitation

The oil and gas industry is ever growing and expanding to deeper depths (Ramirez-Llodra et al. 2011), affecting deep-sea ecosystems (Table 1.1). Construction of oil platforms physically disturbs the deep seafloor, mechanical damage to CWCs can occur during anchoring operations of rigs (Fosså and Skjoldal, 2010; Ragnarsson et al., 2017). During the exploitation face, drill cuttings are released which have been documented to affect deep-sea taxa (Fang et al., 2018; Fosså and Skjoldal, 2010; Järnegren et al., 2020; Kutti et al., 2015; Larsson et al., 2013b; Ragnarsson et al., 2017).

Fossil fuel burning is one of the main causes of climate change (Myhre et al., 2013) that also affects deep-sea ecosystems, as explored below.

1.3.2.3. Deep-sea mining and mine tailing deposition

Interest in deep-sea mining has been growing in recent years due to the growing demand on metals needed to sustain green energy storage (Wedding et al., 2015). This exploitative endeavour and mine tailing deposition at sea can create numerous conditions that affect deep-sea fauna (Table 1.1).

Possible consequences of deep-sea mining endeavours were explored during the disturbance and recolonisation (DISCOL) experiment done in the South Pacific Ocean in 1989 (Thiel et al., 2001). The area has been monitored

throughout the years, and sessile megafauna showed no sign of recovery as of 2015 (Jones et al., 2017).

Table 1:1. Effects of different types of exploitative industries on selected CWCs and deep-sea taxa. Colours indicate the severity of the impact. Pink: high impact, Yellow: medium impact, Green: low impact. The severity of the impacts presented in this table are based on the cited literature and the author´s knowledge.

Exploitative industries											
	Fishing				Oil and Gas			Deep-sea mining mine tailing deposition			
Stony corals	**Smothering** Althaus et al., 2009; Clark et al., 2007 ; Fossa et al.,2002; Hourigan et al., 2007; Ragnarsson et al., 2017	**dislodging/ breakage** Ragnarsson et al., 2017	**Clogging because of excessive sediment ation** Ragnarsso n et al., 2017	**Ghost fishing** Buhl-Mortense n and Mortense n, 2017; Stevens, 2020	**Smothering** Fossa and Skjoldal ,2010; Ragnarsson et al., 2017	**Clogging because of excessive sediment ation** Järnegren et al., 2020; Larsson et al., 2013b	**Oil spills** Girard and Fisher, 2018	**Smothering** Ramirez-Llodra et al., 2015	**Loss of substrate** Boshen et al. 2013; Fukushim a et al., 2000; Levin et al., 2016; Ramirez-Llodra et al., 2015	**Toxicologi cal effects** Levin et al., 2016	**Clogging because of excessive sediment ation** Levin et al., 2016; Liefmann et al., 2018; Ramirez-
Soft corals	**Smothering** Althaus et al., 2009; Clark et al., 2007 ; Fossa et al.,2002; Hourigan et al., 2007; Ragnarsson et al., 2017	**dislodging/ breakage** Ragnarsson et al., 2017	**Clogging because of excessive sediment ation** Ragnarsso n et al., 2017	**Ghost fishing** Buhl-Mortense n and Mortense n, 2017; Stevens, 2020	**Smothering** Fossa and Skjoldal ,2010; Ragnarsson et al., 2017	**Clogging because of excessive sediment ation** Gates and Jones, 2012	**Oil spills** Girard and Fisher, 2018	**Smothering** Ramirez-Llodra et al., 2015	**Loss of substrate** Boshen et al. 2013; Fukushim a et al., 2000; Levin et al., 2016; Ramirez-Llodra et al., 2015	**Toxicologi cal effects** Levin et al., 2016	**Clogging because of excessive sediment ation** Levin et al., 2016; Liefmann et al., 2018; Ramirez-Llodra et al., 2015
Sponges	**Smothering** Althaus et al., 2009; Clark et al., 2007 ; Fossa et al.,2002; Hourigan et al., 2007; Ragnarsson et al., 2017	**dislodging/ breakage** Ragnarsson et al., 2017	**Clogging because of excessive sediment ation** Ragnarsso n et al., 2017	**Ghost fishing** Buhl-Mortense n and Mortense n, 2017; Stevens, 2020	**Smothering** Fossa and Skjoldal ,2010; Ragnarsson et al., 2017	**Clogging because of excessive sediment ation** Fang et al., 2018; Gates and Jones ,2012	**Oil spills** Girard and Fisher, 2018	**Smothering** Ramirez-Llodra et al., 2015	**Loss of substrate** Boshen et al. 2013; Fukushim a et al., 2000; Levin et al., 2016; Ramirez-Llodra et al., 2015	**Toxicologi cal effects** Levin et al., 2016	**Clogging because of excessive sediment ation** Levin et al., 2016; Liefmann et al., 2018; Ramirez Llodra et al., 2015
Bivalves	**Smothering** Althaus et al., 2009; Clark et al., 2007 ; Fossa et al.,2002; Hourigan et al., 2007; Ragnarsson et al., 2017	**dislodging/ breakage** Ragnarsson et al., 2017	**Clogging because of excessive sediment ation** Ragnarsso n et al., 2017	**Ghost fishing** Buhl-Mortense n and Mortense n, 2017; Stevens, 2020	**Smothering** Fossa and Skjoldal ,2010; Ragnarsson et al., 2017	**Clogging because of excessive sediment ation** Gates and Jones, 2012	**Oil spills** Girard and Fisher, 2018	**Smothering** Ramirez-Llodra et al., 2015	**Loss of substrate** Boshen et al. 2013; Fukushim a et al., 2000; Levin et al., 2016; Ramirez-Llodra et al., 2015	**Toxicologi cal effects** Levin et al., 2016	**Clogging because of excessive sediment ation** Levin et al., 2016; Liefmann et al., 2018; Ramirez-Llodra et al., 2015

1.3.2.4. Climate change

Changes in abiotic conditions also threaten the functionality of VMEs and can modulate the dynamics of species interactions. Most notable changes due to climate change are: temperature increase, food supply changes, deoxygenation, changes in ocean circulation, and ocean acidification as explore in more detailed below and (Table 1.2)

1.3.2.4.1. Temperature increase

The ocean will continue to warm and acidify (Figures 1.1 and 1.3). The strongest warming is projected for the surface in tropical and Northern Hemisphere subtropical regions (Bindoff et al., 2019). Increased temperatures affect the metabolism and survival of deep-sea corals sponges, and bivalves (Table 1.2). Multiple studies have been looking at the effect of temperature in CWCs and found contradicting results regarding oxygen consumption. The contradiction can be explained as an acute response in the former study and a chronic one in the latter, or the corals could have acclimated after longer time exposed to higher temperatures.

1.3.2.4.2. Food supply changes

Higher sea surface temperatures enhance ocean stratification and slow mixing, which in turn decreases surface productivity (Behrenfeld et al., 2006; Polovina et al., 2008). Lower phytoplankton production has already been linked to high sea surface temperature and stratified waters (Boyce et al., 2010). Lower production translates to less food for grazing organisms, and potentially, less

particulate organic matter (POM) exported to the deep ocean (Figures 1.3, and 1.4) (Danovaro et al., 2001; Sweetman et al. 2017). Projections show that POM export to the deep sea will significantly decrease (Jones et al., 2014); these changes in flux could negatively affect CWCs and sponge habitats which depend on freshly exported surface POM (Roark et al., 2009; Sherwood et al., 2008; Soetaert et al., 2016). As a result, biomass from deep-sea environments will potentially diminish and areas with CWCs are projected to suffer the greatest declines (Jones et al., 2014). Changes in food availability have the potential to affect the interactions between co-existing VME taxa such as corals, sponges and bivalves but little information is available. Looking at single species, not many studies explore the effect of starvation as a single stressor in CWCs or deep-sea sponges (Table 1.2).

1.3.2.4.3. Deoxygenation

According to the IPCC 2019 report (Bindoff et al., 2019), it is very likely that the dissolved oxygen content of the ocean will decrease by 1 to 7% during the 21st century in response to surface warming, predominantly in the subsurface mid-latitude oceans (Keeling et al., 2009). To date not much is known on how hypoxia would affect CWCs and sponge grounds ecosystems (Table 1.2). Furthermore, temporary extinctions of CWCs in the Mediterranean during the early/mid Holocene have been linked to low O_2 levels (<2ml l^{-1}) (Fink et al., 2012).

1.3.2.4.4. Ocean circulation changes

Weakening (slowing down) of the Atlantic Meridional Overturning Circulation (AMOC) is envisaged over the 21st century, with best estimates and model ranges for the reduction of 11 % to 34 % depending on the different scenarios modelled IPCC 2019 (Collins et al., 2019). This could compromise further oxygen and nutrient supply to the deep sea.

Changes in water circulation patterns represent changes in flow regimes, which in turn affects the distribution of fauna having different feeding strategies, as shown by Wieking and Kröncke (2001). Other studies have shown the effect of different flow regimes in the feeding efficiency of suspension feeders (Orejas et al., 2016; Witte et al., 1997).

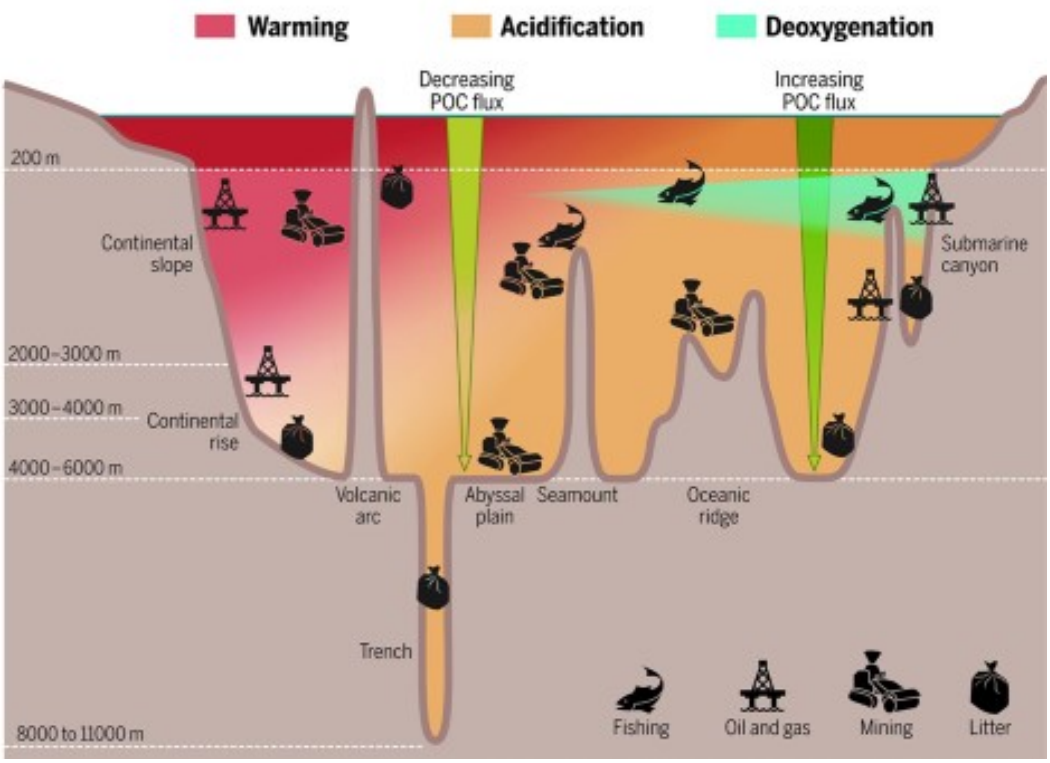

Figure 1.3. Anthropogenic influences of industrial activities and climate change. Figure taken from Levin and Le Bris (2015). © 2015, American Association for the Advancement of Scienc

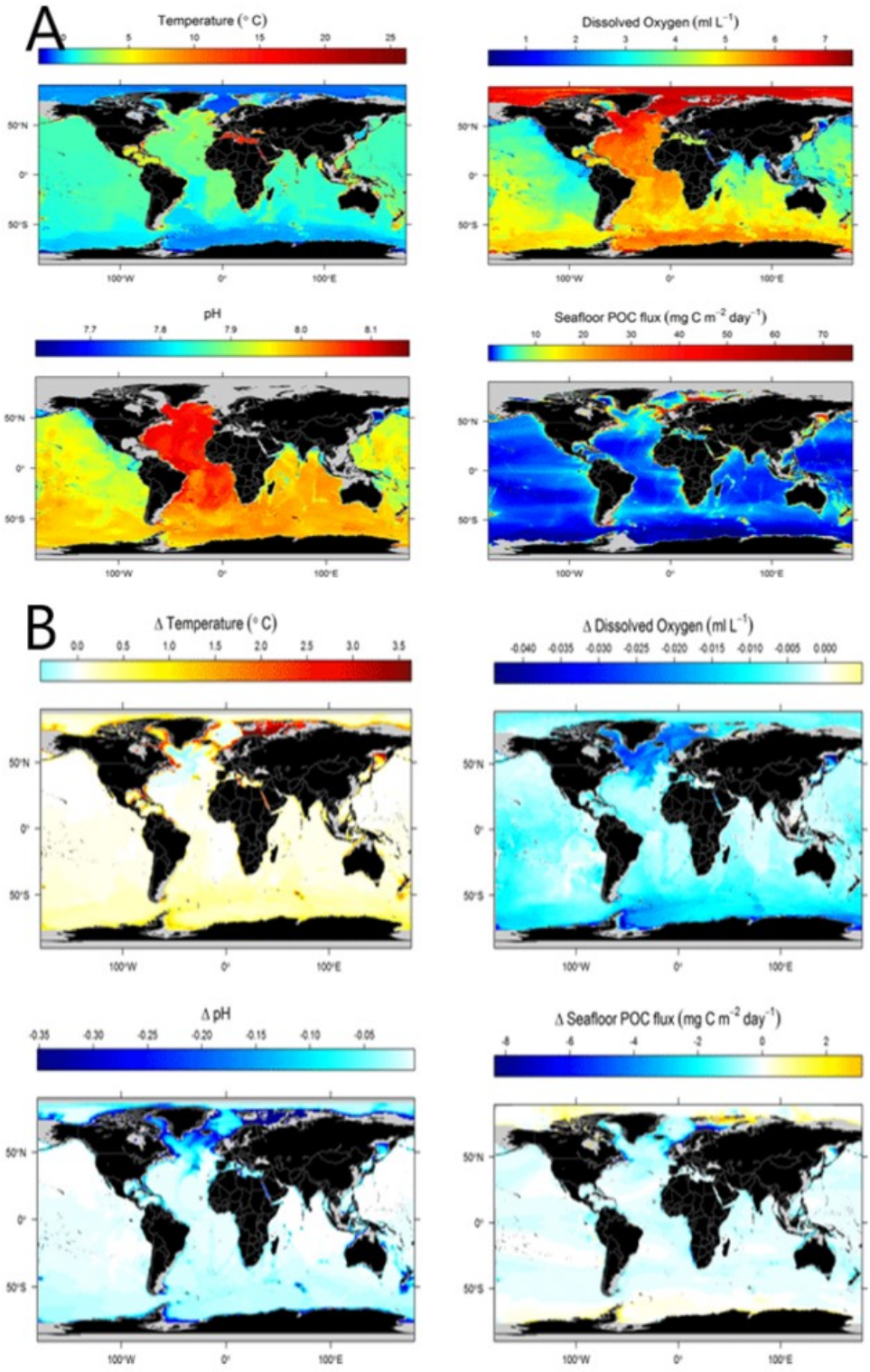

Figure 1.4. (A): Present-day environmental conditions at the deep-seafloor. (B): Modelled environmental changes at the deep-seafloor in the year 2100 relative to present day conditions. Temperature (°C), dissolved oxygen (ml l^{-1}), pH, and seafloor POC flux (mg C m^{-2} d^{-1}) conditions at the deep (> 200 m) seafloor. Figure taken and modified from Sweetman et al. (2017). © 2017, Elementa Science of the Anthropoce*ne*

1.3.2.4.5. Ocean acidification

Another consequence of climate change is ocean acidification due to CO_2 absorption by the ocean water (Figures 1.3 and 1.4), reducing the pH and concentration, and saturation states of the biologically important $CaCO_3$ minerals calcite (Ω_{ca}) and aragonite (Ω_{ar}), which affects several biological processes of VME indicator taxa. Stony corals build their skeletons by precipitating aragonite, bivalves precipitate calcite and aragonite, and octocorals build their skeletons by precipitating calcite, a reduction in Ω_{ca} and Ω_{ar} could limit their distribution (Morato et al., 2020). Several studies have been done to understand the effects of acidification in different aspects of CWCs such as calcification, respiration, and skeletal morphology (Büscher et al., 2017; Hennige et al 2015 and references therein), and for sponges and bivalves (Table 1.2).

Cold-water corals, deep-sea sponges, and bivalves would not be exposed to just one of the aforementioned consequences of climate change, hence the importance of considering multiple stressors and their possible interactions (positive or negative) (Büscher et al., 2017; Gori et al., 2016; Hennige et al., 2015). Vulnerable marine ecosystems are composed of various taxa, the functionality of the whole ecosystems can be shaped by the interactions between the different species. Biodiversity has been documented to be important for maintaining ecosystem functioning (Danovaro et al., 2008) and interactions between the different species can also confer resilience to the ecosystem and can be beneficial for maintaining ecosystem functionality (Hector and Bagchi, 2007).

Thus, it is important to understand the interactions between the different taxa, which can be mediated by the different traits.

Table 1:2. Effects of climate change on selected CWCs, deep-sea sponges and bivalves. Colours indicate the severity of the impact. Pink: high impact, Yellow: medium impact, Green: low impact. The severity of the impacts presented in this table are based on the cited literature and the author´s knowledge.

	Climate change			
	Temperature increase	**Food supply decrease**	**Deoxygenation**	**Acidification**
Lophellia pertusa	**Increased respiration** Dodds et al., 2007		**Tolerant** Brooke and Ross 2014; Dodds et al., 2007; Dullo et al., 2008; Georgian et al., 2016; Hebblen et al., 2020	**Deformities** Buüscher etal., 2017 Hennige et al., 2015
	Decreased respiration Hennige et al.,2015	**Decreased respiration** Larsson et al., 2013		**Decreased growth** Büscher et al., 2017
	Mortality Brooke et al., 2013	**Reduced fitness** Büscher et al., 2017		
Desmophyllum dianthus	**Reduced calcification** Gori et al., 2016	**Decreased respiration** Naumann et al., 2011		**Decreased growth** Movilla et al., 2014
Dendrophyllia cornigera	**Elevated growth** Naumann et al ., 2013			
Paramuricea clavata	**Decreased respiration** Previati et al., 2010			
Eunicella singularis	**Decreased respiration** Previati et al., 2010			
	Decreased polyp activity Previati et al., 2010			
Eunicella cavolinii	**Decreased respiration** Previati et al., 2010			
	Decreased polyp activity Previati et al., 2010			
Corallium rubrum	**Decreased respiration** Previati et al., 2010			**Reduced growth** Bramanti et al., 2013

	Decreased polyp activity Previati et al., 2010			**Reduced feeding** Bramanti et al., 2013
				Sclerite deformities Bramati et al., 2013
Acesta excavata	**Tolerant** Dorey Personal communication			**Resilient**, Hammer et al., 2011
Geodia barretti			**Possible effect on microbiome** Leys et al., 2018	
Radiella hemisphaerica				**Reduced food uptake** Robertson et al.. 2017
Polymastia spp				**Reduced food uptake** Robertson et al.. 2017

1.4. Interactions between VME taxa

Species forming VMEs co-occur and can experience similar conditions, the interactions between the different species and the abiotic conditions are important aspects to take into account to understand the functionality of the ecosystem as a whole. Therefore, understanding the differences of the co-occurring species can help us assess their usage of the available resources, their interactions, and how the different species could react to different flow speeds and changing food concentrations, two aspects projected to change with global warming (Sweetman et al., 2017). These two aspects influence Nutrient cycling, which is an important characteristic of the deep sea and VMEs.

Nutrient cycling is not specifically mentioned in the VME criteria, but it is a major aspect of ecosystem functionality. The FAO criteria for VMEs classify the nutrient cycling under structural complexity because, ecological processes are usually highly dependent on these structured systems. Further, such ecosystems often have high diversity, which is dependent on the structuring organisms. Cold-water corals and sponge grounds are also known to play a role in carbon and nutrient cycling, as they feed from carbon derived from surface water (Sherwood et al., 2008; Soetaert et al., 2016). Respiration and carbon assimilation data also place CWCs and sponge grounds as hot-spot habitats for carbon cycling when compared to soft sediment habitats (van Oevelen et al., 2009). Respiration rates of *L. pertusa* reefs and sponge grounds were 4 to 20 times greater than those of

adjacent soft sediments, reinforcing their role in the biogeochemical cycles (Cathalot et al., 2015; Rovelli et al., 2015).

Sponges show significant filtration rates and can process copious amounts of water daily, e.g. *G. barretti* filters 3000 l kg^{-1} DW (Dry Weight) day^{-1} (Kutti et al., 2013), and they are both efficient sinks of carbon, nitrogen, silicon, and important links between the pelagic and benthic food webs (Maldonado et al., 2015). *Geodia barretti* and its associated prokaryotes have been shown to engage in denitrification and anammox (anaerobic ammonium oxidation) (Hoffmann et al., 2009), which removes inorganic nitrogen from the environment. If denitrification and anammox rates observed in *G. barretti* are common processes in sponges all over the world, then marine areas with high sponge cover may function as significant sinks for inorganic nitrogen (Hoffmann et al., 2009). Pham et al. (2019) estimated that the economic value associated with seawater filtration by the sponges removed by the fishing industry in the Flemish Cap is nearly double the market value of the fish catch. *Acesta exavata* has not been studied as extensively as corals and sponges, but has been documented to have a high clearance rate compared to other bivalves 13.36 l $h^{-1}g^{-1}$ (Järnegren and Altin, 2006), which suggests that this species has an important role in the ecosystem and nutrient cycling.

Trait differences can modulate interactions between VME indicator taxa, hence studying and understanding these differences is important. Traits such as: feeding type, morphology and skeleton composition will be explored in more detailed in the following sections.

1.4.1. Different feeding strategies/traits

Sponge and CWCs are important components of the deep sea, but they have different feeding strategies. Cold water corals are active suspension feeders whilst sponges and bivalves are active suspension feeders with a high filtering capacity. These differences possibly allows them to live in close proximity (Figure 1.5). Their different feeding strategies and distinct feeding apparatus can enable them to feed on particles of different size as discussed in more detail below, thus having different roles in the functioning of the ecosystem. Preferences for active suspension feeders found in the deep sea have been mainly determined with lab reared food (Riisgård, 1988; Witte et al., 1997), but no studies to my knowledge have addressed particle size preference when using naturally occurring food for *L. pertusa.*

1.4.1.1 Active suspension feeders

Sponges and bivalves are active suspension feeders, which actively pump water through their bodies to remove food items. As active suspension feeders, it is likely that passive current-induced filtration is unimportant in sponges (Ludeman et al., 2017; Riisgård et al., 1993). Feeding rates of *Thenea abysorum* and *Thenea muricata* are not believed to be influenced by current speed (Witte et al., 1997). Food availability is thus believed to be a factor mediating pumping rates (Ludeman et al., 2017; Robertson et al., 2017). Complementary to this, a type I functional response, (linear increase in intake rate with food density), has been reported for *G. barretti* when exposed to increasing concentrations of bacteria. However, total organic carbon (TOC) removal did not increase with TOC availability (Leys et al., 2018). Conversely, Møhlenberg and Riisgård (1979) showed that all 19

of the bivalve species they studied could retain 100 % of particles larger than 6 µm.

More recent studies have found blue mussels (*Mytilus edulis*) have a higher retention efficiency of particles between 8 and 11.25 µm between flows of 7 to 20 l h^{-1} (Cranford et al., 2016). Studies also suggest that *M. edulis* can change particle size preference depending on food availability and seasonality (Strohmeier et al., 2015). As a potential decrease on the POM that reaches the deep sea due to climate change (Sweetman et al., 2017) might be accompanied by change in the particle size distribution, it is of vital importance to understand particle size preference in co-occurring species.

1.4.1.2 Passive suspension feeders

CWCs are passive suspension feeders which rely on currents for food supply (Fosså et al., 2004), and have been usually found in locations with fast flow rates (Roberts et al., 2006) and high food rate encounter (Thiem et al., 2006). Several studies have been done in order to understand CWCs feeding physiology and how it is influenced by flow speed, with findings agreeing that *L. pertusa* feeding is most efficient under flows below 7 cm s^{-1} (Orejas et al., 2016; Purser et al., 2010). Polyp expansion behaviour was also greater at low flow speeds between 0.5 and 6.7 cm s^{-1} compared to higher velocities above 15.1 cm s^{-1} (Orejas et al., 2016), meaning that under greater flow rates the corals would be unable to feed efficiently.

Slow flow rates are also believed to be suboptimal; Hennige et al. (submitted) discusses that *L. pertusa* modifies flow and grows according to the so-

called Goldilock's principle where growth occurs under optimal flow conditions: not too fast, not too slow. Recent observational studies support this and link suboptimal flow to the amount of living and dead coral in *L. pertusa* colonies (Vad et al., 2017). Food concentration is also a factor affecting feeding rates since at higher prey concentration, the encounter rates also increase. However, above food concentrations of 1,035 *Artemia* nauplii L^{-1}, *L. pertusa* is not able to further increase its consumption (Büscher et al., 2017; Purser et al., 2010).

The effects of flow on deep-sea gorgonians have not been investigated, but Leversee (1976) investigated the effects of flow in the shallow water gorgonian *Leptogorgia virulata* found that colonies perpendicular to the water flow fed more efficiently, and at flows above 10 cm s^{-1} branches were swept back making it difficult to capture prey. Other examples are discussed in the introductions of Chapters 3 and 4.

1.4.2. Shape difference and skeleton composition

Shape differences and skeletal composition can affect how the different species interact with flow conditions, which can have an effect on the efficiency to catch different food items representing distinct optima for the different species. Different coral morphologies modulate flow differently. Branching corals create eddies, which can enhance particle catch under high flows (Patterson, 1984). Equally, different size of *L. pertusa* patches modulate flow differently, which affects the fate of particulate and dissolved matter, as showed by Mienis et al. (2019). This is further discussed in Chapters 3 and 4.

Octocorals are a very varied taxonomic group (Cairns, 2007: Watling et al., 2011), their morphology and skeletal composition is also very variable and has given rise to different suborders. Sclerites found in the coenenchyme of octocorals also vary amongst taxa and are used for taxonomical classification (Bayer, 1955). Understanding how these differences are related to the hydrodynamic regime the species experience and their distribution is of paramount importance to understand their current distribution and possible changes due to global warming.

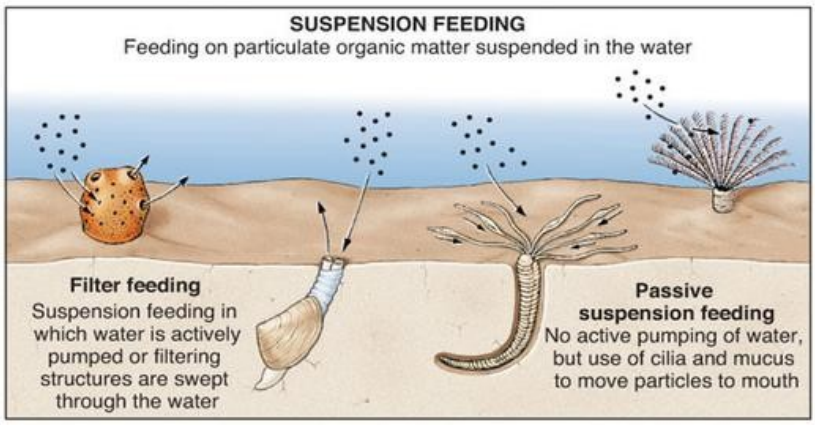

Figure 1.5 Illustration of the difference between active and passive filter feeders. © McGraw Hill companies

1.5. Thesis aims

CWCs and sponge grounds are highly vulnerable to direct impacts from anthropogenic activities such as fishing and deep-sea mining, and their recovery is very slow (Althaus et al., 2009; Buhl-Mortensen et al., 2013). The effects of climate change are not as easily quantifiable and vary between species. Little is known of the feeding ecology of CWCs and sponges, and while long-suspected, their importance for carbon cycling has only recently been demonstrated (Soetaert et al., 2016; van Oevelen et al., 2009). Even fewer studies have been done on the feeding ecology of deep-sea bivalves, but *A. excavata* is believed to be well adapted to low food conditions (Järnegren and Altin, 2006). A key gap remains in understanding how projected changing conditions will affect species interactions with regard to competition and feeding efficiency and how different traits can affect their interactions.

In order to better predict how these ecosystems will respond to climate change it is important to assess their functionality and how the different species interact and how flow can modulate the interactions. In this thesis, species found forming VMEs in the locations in the North Atlantic were used as model organisms to test competition between co-occurring species and the effect flow has on it. The Condor seamount, one of the best studied seamounts in the OSPAR region (Kutti et al., 2019) and is considered amongst the most pristine seamounts (Pitcher et al., 2007). The Condor seamount presents abundant populations of the octocorals *Viminella flagellum*, *Dentomuricea meteor* (Pham et al., 2013) and create coral gardens, thus understanding how

these two species interact and how do they react to changes in flow conditions will help us to better understand their functionality.

The Norwegian Sea harbours different species associations of VME indicator taxa. Variations in species composition are likely dependant on a combination abiotic and biotic factors such as competitive interactions (Järnegren and Kutti 2014). Species associations including *L. pertusa* (scleractinian), *G. barretti*, *Phakellia ventilabrum, Stryphnus* sp. (sponges) and *A. excavata* (bivalve) occur in the Norwegian Sea (Figure 1.1). Hence is important to assess how the different species interact and how flow can modulate the interactions to better understand the stability of the associations and their functionality. Specimens from both sites were collected and their interactions and the effect of flow were tested under laboratory experiments as described in Chapters 2, 3 and 4.

Chapter 2 will explore how skeletal composition and sclerite size and shape can be related to the performance in the environment and the known distribution of two octocoral species found in the Condor seamount, *V. flagellum* and *D. meteor.* Skeletal composition, which underlies axis type, and sclerite type and size are considered functional traits, and can represent adaptations to different flow conditions and depths (Quattrini et al., 2017). Traits can influence species interactions (Webb et al., 2002), therefore understanding how these traits are related to their environment could shed light into the different strategies of co-existent species on resource partitioning and taking advantage of different environmental factors.

Chapter 3 will explore feeding efficiency of *D. meteor* and *V. flagellum* from the Azores archipelago under two different flow regimes. Feeding efficiency will be measured when species are in competition (two species together) and alone in order to understand the interactions between the two co-existent species. The results will be discussed taking into consideration the information gathered in Chapter 2, since differences in traits affects performance and have the capacity of affecting competitive interactions between species (Kunstler et al., 2016; Lavergne et al., 2010; Weither et al., 1998). Overall, the findings will be used to assess which species would be more successful under changing conditions, and how will that affect nutrient cycling and ecosystem functionality.

Chapter 4 will investigate feeding efficiency of VME indicator taxa occurring in Norway: CWC *L. pertusa,* and *A. excavata*, *G. barretti, P. ventilabrum,* and

Stryphnus sp. All these species are key habitat building species found in the North Atlantic, and have different feeding strategies (passive and active suspension feeders). Feeding efficiency will be assessed taking into consideration particle size, type and the effects of environmental variability in the form of three flow regimes, and different concentrations of food particles. Understanding how these species partition food resources under different circumstances will increase understanding of how carbon cycling (e.g. carbon uptake through prey capture, and subsequent respiration) may be altered under changing conditions.

Chapter 2: Biomechanics and structural responses to hydrodynamic flow rate of two octocorals, *Viminella flagellum* and *Dentomuricea meteor* forming VME from the Condor Seamount.

2.1. Introduction

This chapter will explore how different traits present in VME indicator taxa can affect their performance, and how the traits relate to their known distribution.

Corals are a very broad group of organisms, defined as cnidarians having continuous or discontinuous calcium carbonate or horn-like skeletal elements (Cairns, 2007). Taking into account this definition corals encompass seven different taxa Scleractinia, Antipatharia, Octocorallia, Stylasteridae, and Milleporidae, two zoanthids, and three calcified hydractiniids (Cairns, 2007). Corals found in the deep sea, here defined as beyond 50 m depth, belong more commonly to the following groups: Scleractinia and Antipatharia, both belonging to the subclass Hexacorallia, and the subclass Octocorallia (Figure 2.1). Of the 615 scleractinian species found on the deep-sea 74% are solitary and 26 % are colonial, and more than 70% of all scleractinians occur in waters shallower than 1000 m. Anthipatharians are represented with 178 species in the deep sea, and the deepest recorded coral at 8,600 m depth belongs to this order (Roberts et al., 2009). Octocorallia are the most diverse group of corals, with 2,320 species found in waters deeper than 50 m, 67% of the extant families have representatives in the deep sea and have a maximum diversity at depths >200 m (Watling et al., 2011). The orders found in Octocorallia are Alcyonacea, Pennatulacea, Helioporacea. The

most diverse order being Alcyonacea, subdivided into 6 suborders: Proalcyonaria, Stolonifera, Alciyoniina, Scleraxonia, Holaxonia and Calcaxonia (Watling et al., 2011). Since octocorals are more diverse than hexacorals in the deep sea this study will focus on Octocoralia (Figure 2.1).

Morphologically, the Octocorallia are a very diverse group encompassing true soft corals, not having an inner skeleton (Alcyoniina), and those having an inner skeleton: Holaxonia, Calcaxonia and Scleraxonia having branching and whip like shapes. Shape differences are not used to distinguish the different suborders (McFadden et al., 2010), but rather differences in the inner structure of their skeleton, with sclerites used for species identification. The differences in skeleton structure, and sclerite type are considered morphological functional traits (Quattrini et al., 2017) which sometimes correlate with the distribution patterns octocorals display. For example, in the Gulf of Mexico, octocorals found in deeper waters (1300 to 2500 m) are characterised by calcitic skeletons and exhibited more often spindle type sclerites. These deep-sea assemblages belong to the Scleraxonia-Calcaxonia clade as described by Quattrini et al. (2014). More specifically the majority of the species belong to the families Chrysogorgidae and Isididae (Quattrini et al., 2017). Axis type and sclerite shape were traits conserved in octocorals found at those depths, leading Quattrini et al. (2017) to suggest that having a Calcaxonian axis, and rod shaped sclerites as important traits for survival in deeper and colder waters. This difference has been attributed to environmental filtering, meaning that abiotic factors will select for certain traits to persist in a given habitat (Kraft et al., 2015). However, in order to really evaluate to which

extent environmental filtering determines species distribution, several other aspects have to be taken into account (Kraft et al., 2015) such as competition and dispersion barriers. Conversely, on the upper slope octocorals belonging to the Holaxonia- Alcyoniina clade as defined by Quattrini et al. (2014) were more common, particularly those belonging to the family Plexauridae. Quattrini et al. (2017) also observed higher variability in the morphological traits found in deep-sea octocorals observed in shallower depths (250 to 800 m) compared to octocorals found deeper, hinting at phylogenetic and trait evenness (meaning that that local communities are less related and their traits are more different than expected by chance (Pavoine and Bonsall, 2011). Buhl-Mortensen et al. (2015) characterised the distribution of nine deep-sea corals in the North Atlantic and found that from the studied species, two groups of corals could be found, those that were found in water <600 m deep and corals found in waters >600 m deep. The group found in deeper waters was composed by 3 species, *Acanella arbuscula*, from the Isididae family, *Radicipes gracilis* from the Chrysogorgiidae family both belonging to the suborder Calcaxonia, the other species belonging to this group was *Acanthogorgia armata* belonging to the subclass Holaxonia. Buhl-Mortensen et al. (2015) concluded that the depth ranges of the different corals may differ between provinces, depending on the zonation of water masses with different temperatures. Nevertheless, their results could also suggest that octocorals belonging to the Calcaxonia suborder have traits that enable them to persist in deeper colder waters, for example their calcitic skeleton.

Different materials composing octocoral skeletons have different properties and can have an effect on how well suited they are for living/withstanding a particular environment (Koehl, 1999), hence the importance of characterising the elemental composition of the axes. The correlation between skeletal composition and distribution has not been investigated for deep-sea octocorals. Early work done by Esford and Lewis (1987) suggest that the zonation of tropical octocorals was related to stiffness and calcium carbonate content, with stiffer octocorals found in association with calm water regimes, whilst flexible species were more common in surge environments. Other characteristics affecting stiffness of octocorals are sclerite shape, size, and density (Lewis and Wallis, 1991; Koehl, 1977; Prada et al., 2008). Sclerites serve two purposes, they reinforce the tissue and deter predators (West, 1998). While sclerite type is mostly used as a taxonomic characteristic (Bayer, 1955), different sclerites can have different mechanical effects of the flexion of the octocoral skeleton (Lewis and Wallis, 1991). Sclerite size is more labile and has been documented to change through environmental gradients on single species (Grinyo et al., 2018; Prada et al., 2008).

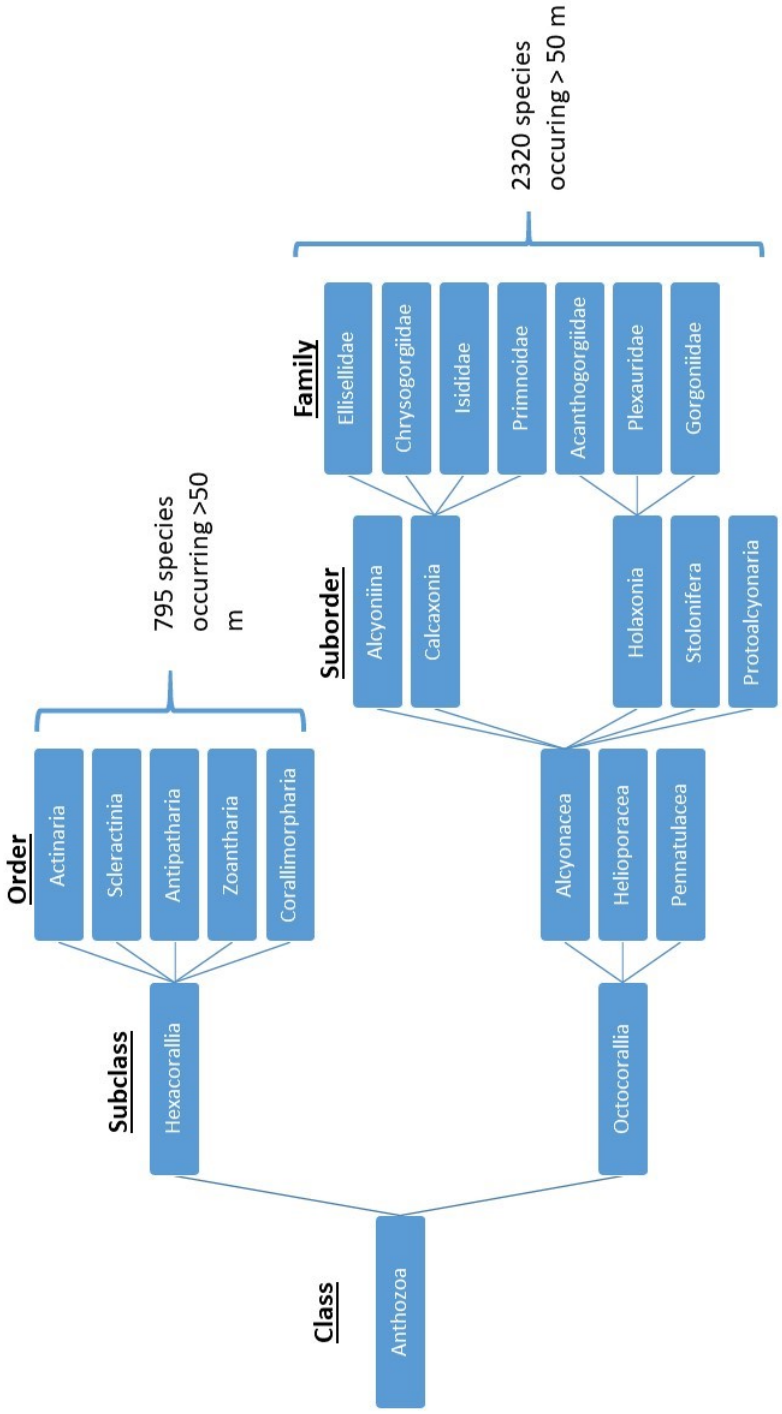

Figure 2.1: Taxonomic tree of corals found in waters deeper > 50 m and the number of species found in each suborder according to Cairns (2007).

Functional traits, performance, and environmental gradients such as depth, can lead to a better understanding of fundamental and realised niches (McGill et al., 2006), meaning that understanding and having knowledge of the aforementioned attributes can help understand the distribution and dynamics of coexisting species. Traits also help identify general patterns, which can help prediction of the dynamics and species distributions under changing conditions (Lavergne et al., 2010; McGill et al., 2006). However, direct links between traits and ecological niches are seldom available (Mouquet et al., 2012), thus choosing traits for their functionality can be a difficult task. Octocoral gardens (See Chapter 1 for a full definition) represent habitats composed of several species. Thus in order to understand the dynamics of these communities, the differences between the species need to be studied and related to their performance and the different abiotic conditions they encounter. For this study traits of interest are axis type and sclerite shape and size. Which vary amongst octocoral lineages.

In the Condor seamount coral gardens are common. Amongst them, bi-species gardens composed of *Viminella flagellum* belonging to the suborder Calcaxonia and *Dentomuricea meteor* belonging to the suborder Holaxonia. Both species have different bathymetric ranges *V. flagellum* ranging fom 90 to 1200 m, and *D. meteor* ranging from 200 to 800 m depth (Braga-Henriques et al., 2013). Equally, *D. meteor* is just found in in the summit of the Condor seamount, whilst *V. falgellum* is found both in the flanks and summit (Tempera et al., 2011) suggesting the two species experience different conditions when not co-occurring. The two species also differ in their overall morphology. *V. flagellum* being a whip

coral reaching up to 3 m in height (Carpine and Grasshoff, 1975), and *D. meteor* a branching coral reaching heights of 50 cm (Sampaio et al., 2008). The diverse conditions they experience when not co-occurring and their morphological differences make them interesting species to study. Assessing their skeletal composition, sclerite type and size and relate it to their known distribution and how it can affect their performance and could give us relevant information to better characterise the niches of the two species. The overall aim of this Chapter is to relate the differences in elemental composition and sclerite size and type of two co existent octocorals to bioimechanics and known distribution. Cross section and longitudinal sections of previously dried skeletons were analysed for elemental composition using Energy dispersive X-ray spectroscopy methods, and they were observed under Scanning electron microscopy. Sclerites were extracted from the tissue of both species and observed under the stereomicroscope and measured.

2.1.1. Aims

More specifically, this Chapter aims to understand:

(i) If the differences in skeletal composition and sclerite shape and size have an effect on to the performance in the environment of the species.

(ii) If skeletal composition, sclerite shape and size can be related with known distribution of *V. flagellum* and *D. meteor*.

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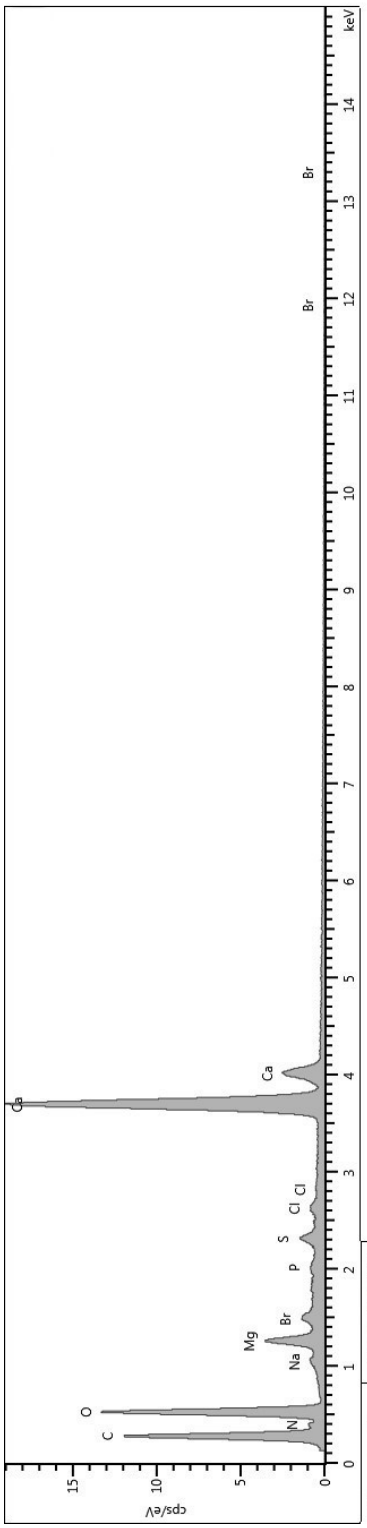
2.2. Materials and Methods

Three *colonies of V. flagellum* and *D. meteor* were collected from the Condor seamount (38°08'N, 29°°05'W) during early 2017 as bycatch from research fishing events from a depth ranging from 179 to 384 m. The fishing method was artisanal longline and was done on board the RV *Arquipelago*. After collection, obtained samples were transported to the DeepSeaLab facilities of Institute of Marine Research (IMAR - Azores)/ Department of Oceanography and Fisheries (DOP) where they were left to air dry. A small branch from each of the three obtained colonies for each species was cut and shipped to the University of Edinburgh for Scanning Electron Microscopy (SEM) and Energy dispersive X-ray spectroscopy analysis using the SEM as an electron beam source.

Energy dispersive X-ray spectroscopy (ED-X) is an analytical technique used to investigate the elemental composition of a sample. When the electron beam of the SEM interacts with a sample it displaces electrons from the innermost electron shell of the atoms another electron from an outer shells replaces it. During the process X-rays are emitted, their energy is equal to the difference between the ionisation energies of the electrons involved in the transition. Hence the X-ray are characteristics of each element. The X-rays are detected by an Energy Dispersive detector which displays the signal as a spectrum, or histogram, of intensity. The elements present in the samples are identified by the energy emitted by the X-rays, while the intensities/counts of the X-ray peaks (Figure 2.2) allow the concentrations of the elements to be quantified. Results are given as element weight percentage.



Element	Weight %
C	22.07
N	8.48
O	35.86
Na	0.22
Mg	1.93
P	0.14
S	0.67
Cl	0.32
Ca	26.97
Br	0.81
I	0
Total	97.45

Figure 2.2: Graph showing the spectrum of the elemental composition of V. flagellum. The y axis represents the counts s^{-1} per electron volt for every element found in the sample. The x axis shows the accelerating voltage range. The table shows the quantification done by the software of the intensity/counts weight percentage of the found elements.

2.2.1. Sample preparation

Upon arrival samples were stripped of the dry tissue with a scalpel, cross sections, and transversal cuts of each sample were made with a diamond saw. The subsamples were then embedded in resin and polished to expose the coral surface and attain a smooth surface. The embedded samples were put in an aluminium support stubs, then coated with a 5 nm thick carbon layer. To make contact with the aluminium stub and the resin embedded sample 3 lines were drawn from top of the samples to the stub with silver paint. Whole pieces of the skeleton material were also glued to an aluminium stub using carbon sticky pads, carbon tape was used to envelop the bottom part of the skeleton to electrically ground the skeleton pieces to the stud. Samples were then placed inside the vacuum chamber of a Carl Zeiss SIGMA HD VP Field Emission SEM with Oxford AZtec ED X-ray analysis equipped with a selective backscatter and a silicon-drift energy dispersive X-ray detector. The accelerating voltage was set at 15 kv, the aperture was set to 30 µm. When acquiring the ED-X profiles the working distance was set a fix to 7 mm. An average of 15 ED-X measurements were taken for each cross section sample, totalling 45 measurements per species. For the transversal cuts and the whole skeleton samples an average of seven measurements per sample were taken. Pictures of the samples were taken to see the internal organisation of the skeleton, equally pictures were taken of the area where the ED-X analysis were performed. Pictures taken of the whole cross section using the SEM were used for sclerochronology. The visible rings of the octocorals were counted, the rings were of unknown periodicity, but assumed to be yearly. The diameter of each cross

section was measured using Image J software (Rasband, 2018). To calculate yearly radial growth the measured diameter of each cross section was divided by their respective amount of counted rings.

The remaining tissue was dissolved in NaClO (sodium hypochlorite) in order to extract the sclerites. The tissues were left to digest until the sclerites were seen as precipitate and all the tissue was dissolved. The precipitate and the solution were then filtered through a Whatman category 1 filter and subsequently rinsed with de-ionised water. The sclerites were left to dry at ambient temperature and then observed under a stereo microscope ZEISS discovery V20. Pictures were taken with an axio 105 camera coupled to the stereo microscope. Pictures for each species were analysed using Image J software (Rasband, 2018). Length and width were measured for 97 sclerites for *V. flagellum* and 81 for *D. meteor*. The sclerites were also categorised according to their shape according to Lewis and Wallis (1991) and Bayer (1983).

One piece of the remaining skeletons of both species was treated with decalcifying solution (Thermo scientific) for 3 days, changing the solution daily in order to remove the calcitic portion of the skeleton. A different skeleton piece was treated with NaClO to remove the organic portion of the axes. This process lasted for 24h for *D. meteor,* until all the tissue was dissolved*,* and 2 weeks for *V. flagellum,* until majority of the organic material had dissolved. These two processes were done in an attempt to see how the different layers of calcitic and organic material were arranged. After the etching process, the remaining of the

skeleton were analysed and photographed with the stereomicroscope and its attached camera (see above).

2.2.2. Data analysis

Measurements that presented a low total mass (under 70%), meaning the sum of all the found elements accounted for less percentage than 70 %, were excluded, results having a total mass percentage above 100% were examined carefully. Cracks and uneven surfaces on the samples can inflate the weigh percentage of certain elements, especially carbon since the polished sections were carbon coated. Hence if the carbon percentage was above 50%, and the image of the sample did not reveal a crack, a hole filled with resin, or a very uneven surface, the results were kept. Data points coming from the sample from both transversal and cross-sectional cuts were averaged. Total Ca and Mg contents and Mg/Ca ratio were also calculated in order to have a proxy for calcitic material and the amount of magnesium inclusion in the calcium carbonate (Jeyasuria and Lewis 1987).

Statistical analysis were done with R studio statistical software version 5.3.1 (R Core team, 2018). Welsh t-test were performed to compare the weight percentage of each found element between the two species. Tests were also performed to compare the elemental weigh percentage between the cross section and the whole skeleton preparations in order to compare the elemental composition of the inner skeleton and the cortex of the same species.

2.3. Results

The SEM pictures of the cross section of the axial skeleton revealed structure in accordance with their sub orders/axis types. *Dentomuricea meteor* belongs to the suborder Holaxonia, having an axis mostly made of scleroproteins with a hollow centre (Figure 2.3 A, Table 2.1). The ED-X confirmed this and analysis from the midle of *D. meteor* axis revealed that the material present was filled with resin, evidenced by a C content above 90%. Some calcitic instrusions where observed on the SEM images (Figure 2.4). *Viminella flagellum* is part of the suborder Calcaxonia presenting a more calcitic skeleton (Watling et al., 2011, which was confirmed by ED-X analysis (see below) (Figure 2.3 B).

The three cross sections of *D. meteor* diameters of 1.3, 1 and 1.2 mm of diameter were measured and 15, 11, and 12 growth rings were counted respectively. The average radial growth rate of *D. meteor* was 0.11 ± 0.008 mm $year^{-1}$. *Viminella* flagellum presented diameters of 0.9, 0.7 and 3.4 mm , the respective counted growth rings 37, 23 and 44. The average radial growth of *V. flagellum* was 0.05 ± 0.03 mm $year^{-1}$ (supplemetary material 2.1).

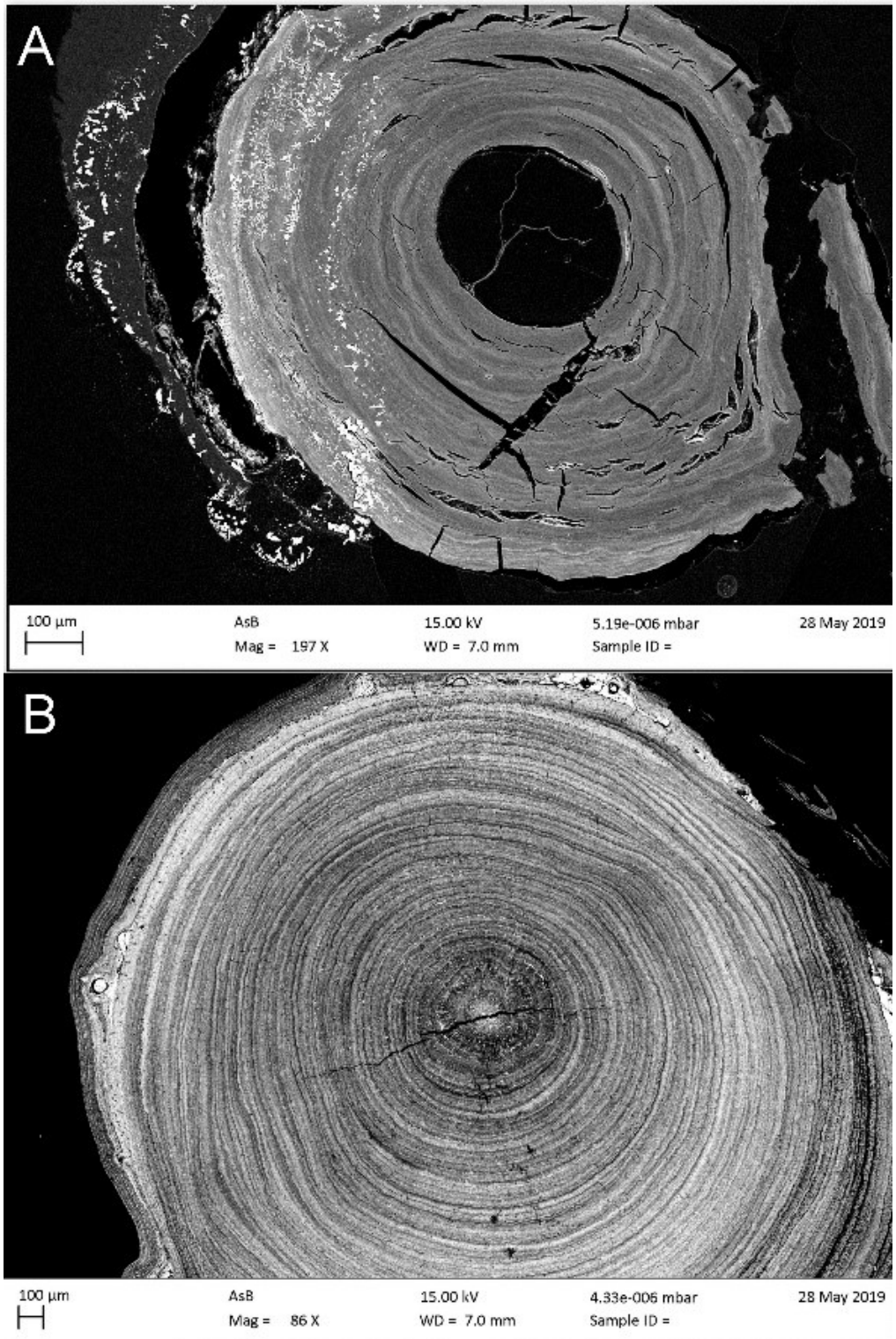


Figure 2.3 SEM images of skeletal cross sections. (A): Cross section of *D. meteor* axis the hollow centre in the middle can be observed, the cracks in the sample were as a result of desiccation and embedding process. (B): *Viminella flagellum* cross section the concentric layers are observable, for sclerochronology see supplementary material 2.1.

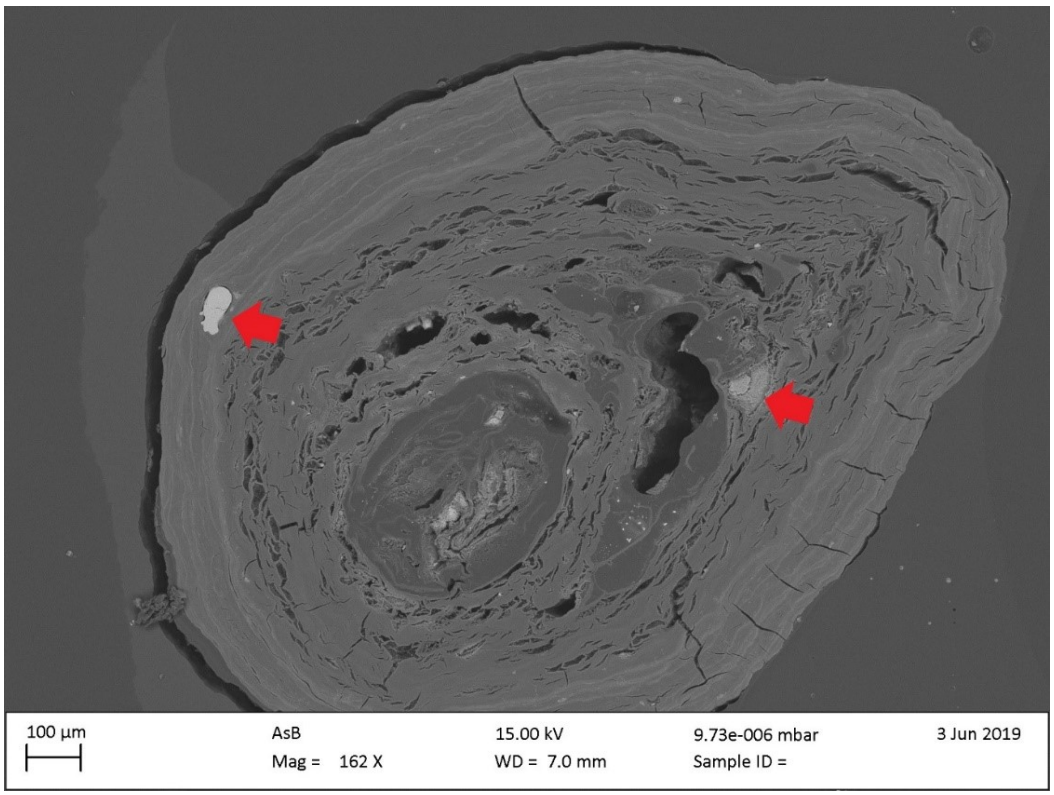


Figure 2.4. SEM image of *D. meteor* skeleton cross section. Arrows point to calcitic intrusions.

Elemental analysis revealed the average composition shown in Table 2.1. *Dentomuricea. meteor* presented significatly higher weight percentage of C, N, P, S, Br and I (p-values < 0.05) than *V. flagellum*. *Viminella flagellum* on the other hand exhibited a higher weight percentage of O, Mg, Ca (p-values <0.05) than *D. meteor*. The calculated Mg/Ca ratio did not show any statistically significant difference, but a trend can be observed where the ratio is higher for *D. meteor* (see discussion).

For *V. flagellum,* comparisons between the axis cortex and the cross section composition of the axial skeleton (Table 2.1) did reveal a significantly higher P percentage weight in the cortex, and a significatly higher Br percentage weigh in the cross section than in the cortex (p-values 0.025 and 0.038

respectively). For *D. meteor* the cortex contained significantly more Mg than the cross section (p-value: 0.005). The cortex of *D. meteor* did not contain P, but the levels of the cross section were very low, close to the detection limit of the instrument.

Table 2.1: Elemental composition of the skeleton cross sections and cortex of D.meteor and V.flagellum. Results are presented as percentage weight and are given as average ± standard deviation.

	Dentomuricea meteor		***Viminella flagellum***	
	Cross section	**Cortex**	**Cross section**	**Cortex**
C	50.55 ± 2.98	65.41 ± 11.85	21.68 ± 3.09	25.98 ± 0.63
N	9.86 ± 1.03	5.44 ± 3.89	5.72 ± 0.14	6.40 ± 0.59
O	19.60 ± 2.46	20.31 ± 6.47	39.98 ± 3.05	48.25 ± 9.28
Na	0.31 ± 0.02	0.63 ± 0.15	0.30 ± 0.03	0.62 ± 0.10
Mg	0.11 ± 0.01	0.41 ± 0.00	2.23 ± 0.25	2.79 ± 0.26
P	0.03 ± 0.03	0.00 ± 0.00	0.13 ± 0.04	0.27 ± 0.03
S	1.76 ± 0.51	0.95 ± 0.07	0.51 ± 0.08	0.65 ± 0.07
Cl	1.34 ± 0.48	2.13 ± 0.72	0.32 ± 0.04	0.97 ± 0.07
Ca	0.75 ± 0.49	0.27 ± 0.11	28.84 ± 2.13	30.16 ± 1.51
Br	5.21 ± 0.09	8.25 ± 2.09	0.64 ± 0.12	0.06 ± 0.04
I	4.93 ± 1.62	8.73 ± 3.99	0.04 ± 0.02	0.39 ± 0.55
Ca+Mg	0.86 ± 0.48	0.68 ± 0.10	31.07 ± 2.38	32.95 ± 1.77
Mg/Ca	0.65 ± 0.12	1.69 ± 0.68	0.08 ± 0.00	0.09 ± 0.00

The skeleton of *D. meteor* dissolved completely after 24 h submerged in NaClO, with few sclerites found in the precipitate. After three days in the

decalcifying solution, the skeleton did not show observable changes when examined under the stereomicroscope. After 24h hours in NaClO the calcitic part of the *V. flagellum* skeleton started to peel off while the organic part dissolved, after two weeks the whole organic part had not yet completely dissolved. After the decalcifying process *V. flagellum* skeleton was found to have softened and had a leathery consistence with a dark brown colour. The concentric organisation was still noticeable, and there was no sign of calcitic material remaining. The decalcified skeleton of *V. flagellum* showed twisting fibres as opposed to straight patterns observed in the calcitic material (Figure 2.5).

Dentomuricea meteor presented different types of sclerites: scaphoids, spindles, thornscales, corallet spindles and radiates (Figure 2.6), mean sizes are presented in Table 2.2. Spindles were the more abundant, representing 54.3%. *Viminella flagellum* had the following sclerite types: double heads, radiates, and spindles (Figure 2.7) mean sizes are presented in Table 2.2. The most abundant type were double heads representing 48.5%. Overall *D. meteor* had bigger sclerites than *V. Flagellum* (for comparison see Table 2.2).

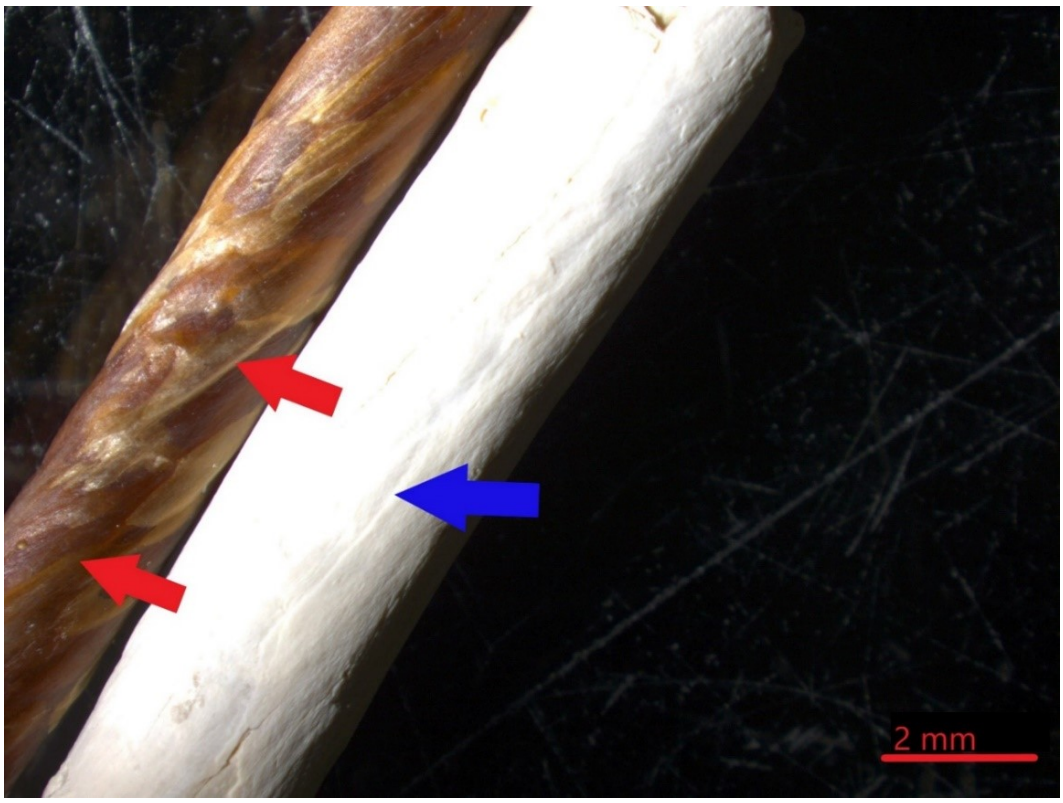


Figure 2.5: *Viminella flagellum* skeleton. The brown skeleton shows the result of the decalcifying process. The red arrows point to the diagonal arrangement of the gorgonin fibres. The white skeleton shows the result of the NaClO treatment. The blue arrow points to the parallel to the axis arrangement of the calcitic material.

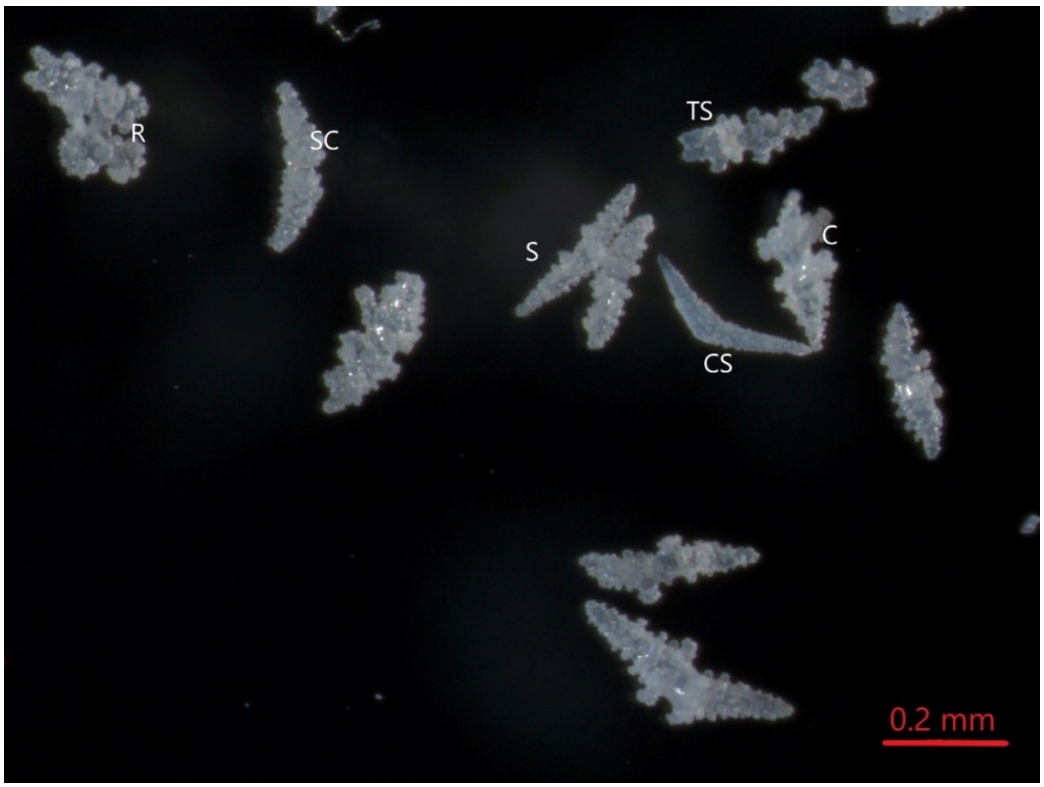


Figure 2.6: Sclerite types present in *D.meteor*. R: radiate. SC: Scaphoid: TS: Thornscale. S: Spindle. C: Club. CS: Corallet spindle.

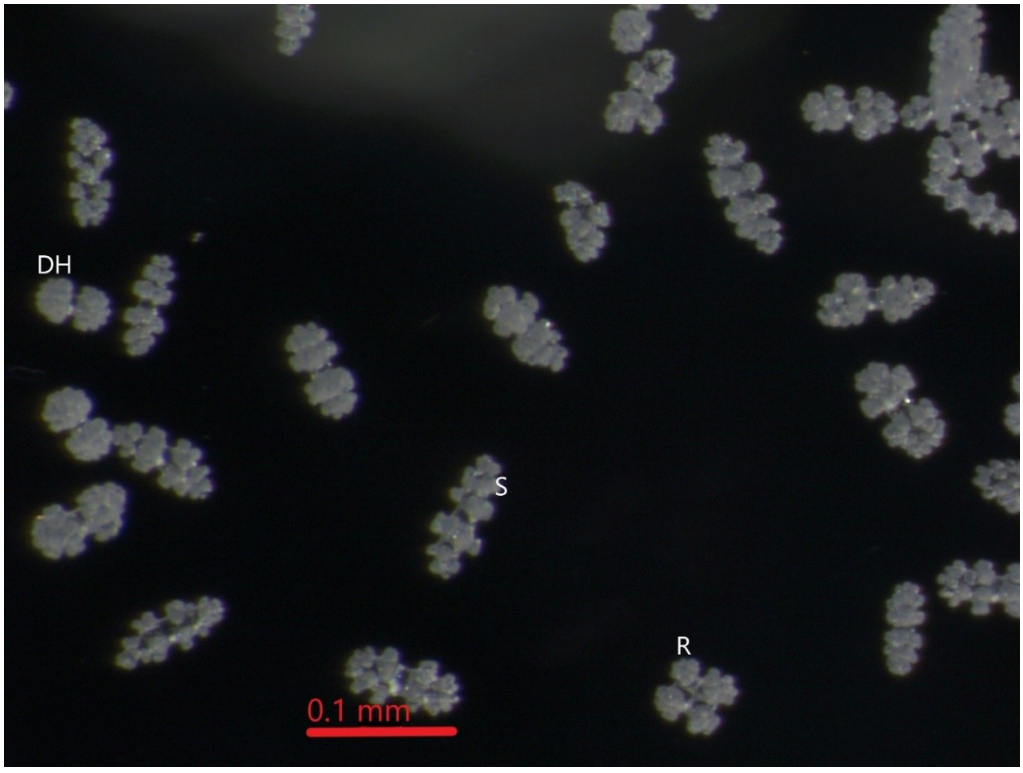


Figure 2.7. Sclerite types present in *V. flagellum*. DH: Double head. S: Spindle. R: Radiate.

Table 2.2: Dimensions of sclerites found in the coenenchyme of *D.meteor and V. flagellum*, results are presented as average ± standard deviation in mm.

Species	**Type of Sclerite**	**Length mm**	**Width mm**
Dentomuricea meteor	clubs	0.22 ± 0.04	0.09 ± 0.02
	corallet spindle	0.33 ± 0.14	0.06 ± 0.02
	radiates	0.18 ± 0.12	0.05 ± 0.03
	scaphoids	0.27 ± 0.06	0.09 ± 0.03
	spindles	0.26 ± 0.06	0.09 ± 0.03
	thornscales	0.32 ± 0.09	0.13 ± 0.06
Viminella flagellum	double heads	0.07 ± 0.01	0.04 ± 0.01
	radiates	0.16 ± 0.11	0.05 ± 0.04
	spindles	0.08 ± 0.01	0.04 ± 0.01

2.4. Discussion

The calculated radial growth for both *D. meteor* and *V. flagellum* are based on assumed yearly growth rings. Nevertheless, the radial growth rates were low, which validates coral gardens composed of these two species as VME indicator taxa according to the life history trait criteria.

2.4.1.Effect of skeletal composition and sclerite shape and size in biomechanics

2.4.1.1. Relating skeletal composition to mechanical properties

Viminella flagellum has a highly mineralised skeleton with over 30% of Ca + Mg whilst *D. meteor* has a skeleton composed of under 1% Ca + Mg, this could hint that *V. flagellum* has a more rigid skeleton having a higher of $CaCO_3$. As pointed out by Jeyasuria and Lewis (1987), and Esford and Lewis (1990) carbonate content can be correlated with stiffness. The fact that *V. flagellum* has a higher percentage of Ca + Mg in its skeleton might indeed mean that it is stiffer than *D. meteor*. Anecdotally when handling skeletons of both species *D. meteor* seemed more flexible (Liefmann, personal communication). This is the base for further investigation because several parameters can affect the mechanical properties of the skeleton (Hennige et al., 2020).

The levels of Ca and Mg found in the two species are in accordance with the results found by Weinnig (2015) for species belonging to the same families, but Weinnig just examined one species belonging to each family, Plexauridae and Ellisellidae. Other studies evaluating this, found a higher variability on the Ca + Mg contents in the axis of Pleaxauridae octocorals ranging from 23% to 0.01% (Esford and Lewis, 1990). This variation should come as no surprise since the family of Plexauridae has been documented as one of the more diverse and abundant

within octocorals, presenting 47 genera (Cordeiro et al., 2020; Sampaio et al., 2019 b). Higher percentage of Mg in calcium carbonate produces a harder and tougher material (Jeyasuria and Lewis, 1987), thus the small difference found in the Mg/Ca ratio between the two studied species could mean that *D. meteor* has a slightly tougher $CaCO_3$.

Dentomuricea meteor presented higher levels of halogens, especially iodine. The presence of this element can be possibly explained by the fact that it has been linked to the binding of scleroproteins, in this case gorgonin (Ehrlich, 2019; Szmant-Froelich, 1974). Hence a more organic skeleton would be expected to have more binding agents. The same relationship was found by Weinnig (2015), the author found that all the analysed species that exhibited high percentage of Ca and Mg had very little or no halogens in the skeleton.

The present study did not measure stiffness, and assumptions were made from the author experiences when handling the corals and by $CaCO_3$ content, as previously mentioned, several parameters have to be taken into account when measuring stiffness. As mentioned by Lewis et al. (1992) $CaCO_3$ content is not the only parameter that affects stiffness. For example Lewis et al. (1992) found that the stiffness measured for *Plexaurella* spp and *Lophogorgia cardinalis* presented similar young modulus values (stiffness coefficient, the higher, the stiffer the material) 35 and 40 Gdyne $^{1}cm^{-2}$ respectively, meaning that *L. cardinalis* is stiffer.

[1] Giga Dyne. A dyne per square centimeter (dyn/cm^2) is the Centimetre–gram–second derived unit of pressure, stress, Young's modulus and ultimate tensile strength.

Nevertheless, when looking at the Ca + Mg content *Plexaurella* spp has almost double concentration of Ca and Mg.

Other parameters such as crystallisation, gorgonin and collagen fibres organisation can also mediate the stiffness. However, these two parameters have not been given much attention in deep-sea octocorals. Stiffness has usually been measured for the axis of different octocorals by means of the bending beams methods as described in (Stephenson, 1969) and using rehydrated skeletons, which could vary compared with alive fresh skeletons. The bending beams methodology assumes a beam that has the same shape all along and that has isotropic qualities (Roark, 1943), meaning the material properties are not directionally variable (Etnier, 2003), which might not be the case. Especially when taking into consideration that top parts of the skeleton are younger material, meaning the width along the beam is not the same. Further, cross sections of octocoral skeletons are not uniform, as observed for the two species studied where the distribution of the materials is seemingly not uniform.

2.4.1.2. Relating sclerite size and shape to mechanical properties

Stiffness and other mechanical properties of the octocorals, are not just dictated by the properties of the axial skeleton. The coenenchyme enveloping the skeleton contains sclerites, and the coenenchyme sclerite “wrap” has been shown to affect the stiffness of shallow water octocorals to a varying degree, depending on the species (Esford and Lewis, 1990; Lewis and Wallis, 1991). It has been further hypothesised that the orientation and shape of the sclerites has an effect on the mechanical properties (Muzik and Wainright, 1977)

The type of sclerites found in the two species studied was different, *V. flagellum* having predominantly double heads, as it is characteristic for the Ellisellidae family (Carpine and Grashoff, 1975; Giusti et al., 2012) while *D. meteor* exhibited predominantly spindles, which is characteristic of Plexauridae (Carpine and Grashoff, 1975). Even if sclerites are commonly used as a taxonomic feature, their different shapes and morphologies reveal different functionalities and confer different properties to the colony as a whole. For example, Lewis and Wallis (1991) examined the roles of different types of sclerites and came to the conclusion that double heads limit movement in all directions. The spindles studied by Lewis and Wallis (1991) were on the surface, and their function was suggested to be support of the polyp. Conversely the spindles of *D. meteor* are usually found in deeper layers of the coenenchyme (Grasshoff, 1977) so it is difficult to make parallels with the findings of Lewis and Wallis (1991). No function has been attributed to spindles found in the deep layers of the coenenchyme, but it has been suggested that they can interact with surface clubs to enable torsional forces to be transmitted (Lewis and Wallis, 1991).

Taking into account the available knowledge on the functions of sclerites it can be suggested that the double head sclerites present in *V. flagellum* could reinforce its stiffness. Equally, the spindles present in *D. meteor* could enhance their rotational ability while linking with the surficial sclerites, which are usually clubs and thornscales (Grasshoff, 1977). The role of thornscale sclerites has not been discussed in the literature, but it is possible that they can interlock with spindles in order to transmit rotational forces. One of the functions of spindles has

been hypothesised to help/enhance flexibility of the octocorals (Skoufas et al., 2006).

The role of the coenenchyme in the mechanical properties of octocorals should be more important in species presenting a thick coenenchyme with densely and tightly packed sclerites layers such as *D. meteor* (Grasshoff, 1977). The way the different layers interact and affect the mechanical properties of the octocorals is not well known (besides spindles and clubs interactions), but they are believed to be complicated (Lewis and Wallis, 1991). Further research for understanding how sclerites interact with each other, and the tissue could help the scientific community to grasp the effect that the coenenchyme sclerite wrap has on the mechanical properties of the different species.

2.4.1.3. Relation of mechanical properties to hydrodynamics

Jeyasuria and Lewis (1987) related the stiffness of the octocoral axis to the current regime different species were exposed to. They found that corals present in the surge zone tend to have a more flexible skeleton when compared to skeletons of octocorals found in environments where more steady currents dominated. This suggests that having a stiffer skeleton is biomechanically better in moderate flow conditions, while having a flexible skeleton is biomechanically better for surge /high flow environments. Following this argument, it could be suggested that *V. flagellum* could be better suited for moderate flow environments, and *D. mete*or could be better adapted to high flow conditions.However, colony morphology could indicate the opposite, since whip

like shapes such as *V.flagellum* have less resistance to water flow than branching forms such as *D. meteor,* indicating a possible trade-off between morphology and stiffness. Later Esford and Lewis (1990) postulated that the relationship between water regime and stiffness was not as straight forward as previously taught. However, deep-sea systems do not experience surge type water flow, so direct comparisons between octocorals from the deep-sea and tropical environments having a flexible skeleton/axis can be difficult.

The mineral and organic layers in the skeletons of *V. flagellum* were found to have different directionalities. The observed differences suggest that the distinct layers can confer resistance to two different forces, the diagonal gorgonin fibres might act tackling twisting (torsional) forces, and the calcium carbonate layers could confer flexural stiffness, which can be advantageous when experiencing different water regimes. Regarding *D. meteor*, judging skeletal composition and inferring properties from a small sample might not be the best course of action, since it is a branching octocoral and the different branch orders of other gorgonians have been documented to have different stiffness coefficients (Esford and Lewis, 1990). For example, species where the axial skeleton was mainly organic were found to have a more calcified stem and holdfast in order to withstand drag forces (Bayer and Mcintyre, 2001). Different parts of the skeleton can react differently to distinct hydrodynamic regimes.

In order to properly understand stiffness and other important mechanical properties of the octocoral skeletons, more parameters such as hardness

toughness, and anisotropy should be taken into account. Equally other techniques, and models should be used so that all the skeletal features are taken into consideration, for example nanoindendation technique as described by Fransozo and Zysset (2009) and Hennige et al. (2020). Additionally, whole colonies should be studied when assessing the mechanical properties, as morphology also affects how corals interact with their environment and their overall mechanics as discussed in Chapter 3.

Another aspect that has not been taken into account in the past is that other forces with different directionalities can work upon coral skeletons, for example hydrostatic pressure, which will excerpt an increasing force with depth in the skeleton on top of the axis. Other parameters beyond simply torsion and flexural stiffness should therefore be taken into account when assessing octocoral skeletons performance.

The mean sclerite sizes also differed between *V. flagellum* and *D. meteor*, direct comparison between the sclerite sizes of the two species has little sense because they exhibit different types having different functions. To this day, this type of comparison has been done intraspecifically, or with very similar species in order to detect phenotypical plasticity or possible speciation (Prada et al., 2008). Skoufas et al. (2006) hypothesised that spindles from *Eunicella singularis* inhabiting shallow more exposed sites were longer because they help the coral come quick to an upright position after being swept by impinging currents. Skoufas (2006) results are in accordance with observations from Gori et al. (2012) and

Velimirov (1976) (all the aforementioned observations were done in species occurring in the Mediterranean Sea). On the other hand, studies done on shallow-water octocorals from the Caribbean Sea observed bigger sclerites from deeper colonies, and smaller ones in colonies from shallow water (West et al., 1993; Kim et al., 2004; Prada et al., 2008). Smaller sclerites found in shallow more dynamic environments were discussed as a possible adaptation to high water motion, since large sclerites are more susceptible to breakage than smaller ones (West, 1998).

2.4.2. Relation of the species known distribution to their traits

Viminella flagellum and *D. meteor* when found in mixed gardens, tolerate very similar flow regimes, the question will perhaps be: what is the threshold of each of the skeletal designs and properties? In addition, if the different designs might be adapted to the dynamic /changing conditions encountered in the Condor seamount. Water speeds in the summit of the Condor seamount, where both species co-occur can vary between 2 and 6 cm s^{-1} (Bashmachnikov et al., 2013; Rovelli et al., in preparation). Seamounts create specific conditions that can change flow regimes, and specific regions of the seamounts can experience different hydrodynamic conditions along the mount, for a review see Lavelle and Mohn (2010), and more specifically for the Condor seamount (Bashmachnikov et al., 2013). As an example tidal waves are transformed by the seamount topography into internal waves, which can result in increased fluid shear and turbulence over the summits (Lavelle and Mohn, 2010).

According to the known records of the two species, *V. flagellum* has a larger depth range spanning from 90 to 1200 m in the Azores region and it is found

both in the summit and on one location in the northern flank of the Condor seamount (Braga-Henriques et al., 2011, 2013; Tempera et al., 2011). The Northern flank of the Condor seamount experiences current speeds between 0.6 and 2.6 cm s^{-1} which are lower than the ones reported for the summit (Bashmachnikov et al., 2013). In the Mediterranean Sea *V. flagellum* is reported to prefer moderate water flows (Cau et al., 2015, 2017; Giusti et al., 2012, 2017). The apparent preference of *V. flagellum* for moderate flow speeds and its tolerance for deeper depths suggest that its stiffer skeleton is advantageous, to provide support for the feeding polyps (Muzik and Wainrigth, 1977). *Dentomuricea meteor's* known depth range is 200 to 800 m and is documented to be just present in the summit of the Condor seamount (Braga-Henriques et al., 2013; Porteiro et al., 2013; Tempera et al., 2011) where flow regimes are characterised by high speeds up to 6 cm s^{-1} in average (Amorim at al., 2016; Bashmachnikov et al., 2013). Under these regimes, it could be more beneficial to have a more flexible axis. More flexible skeletons are believed to be better adapted to more "energetic" flow environments i.e. surge, in this type of regimes, the skeleton should be sufficiently flexible in order to avoid snapping, also more flexible structures reduce the drag forces experienced by the axis/skeleton (Koehl, 1984; Muzik and Wainrigth, 1977). The flexed skeleton could also position the polyps better in order to catch prey under high flow regimes (Harvell and La Barbera, 1985, Koehl, 1977).

The two studied species co-exist and experience the same flow regimes, but have two different skeletal strategies. As mentioned by Koehl (1996), strategies that seem to be mechanically detrimental for a species do not

necessarily mean that they do not work in favour of the life strategy followed by the concerned species. Koehl (1999) exemplified this very clearly by studying two different seaweeds living in similar environments one having a “poor” design having weak stipes and holdfasts, but is opportunistic (r-life strategy) and reproduces periodically before seasonal storms hit. On the contrary kelp having stronger stipes and holdfast, ”good” design, can stand storms better, but reproduces seasonally, hence it has to be able to withstand the storm period and invest more in its offspring (k-life strategy). Brittle coral skeletons found in wave swept areas might also seem as a bad mechanical strategy, but it has been shown that several species use this as a strategy for asexual reproduction, presumably via fragmentation (Lasker, 1984; Tunnicliffe, 1981).

Coexisting octocorals can adopt different strategies to tackle drag forces from the impinging water currents. Octocorals could withstand the forces by building a tougher skeleton, or they could minimise the experienced forces by having a flexible skeleton (Lin and Dai, 1996). The different strategies could be adapted to the life history and feeding preferences of the different species. The different traits could also represent trade-offs made by the different species such as drag force reduction vs food acquisition (Harvell and La Barbera, 1985). Trade-offs have also been evidenced for plants (Kunstler et al., 2016; Wright et al., 2010). As off now, there is a gap in the knowledge of the life strategies and overall ecology of CWCs and the two studied species.

The differences in sclerite shape and size encountered in the two species are harder to relate to their known ranges. The double head sclerites found in *V. flagellum* are believed to limit movements in all directions. Hence, sclerites limiting movements could possibly support polyps in low flow environments where the coral is found. On the contrary, the big spindle sclerites found on *D. meteor* could be used for predator deterrence, especially taking into consideration that its coenenchyme is thicker which might make the coral more palatable, though predation on *D. meteor* has not been documented.

Given the complexity of coral skeletons other properties such as toughness and strength, anisotropy/isotropy also mediate the biomechanical properties, these properties should be studied in more detail in order to better understand the functionality of the skeletons and how are they adapted to the different conditions the corals experience.

More traits should studied, since they can have synergistic effects and affect the octocorals performance (Koehl, 1996). Intraspecific trait variation should also be accounted for, in order to perceive the full range of the species, phenotypical variation in sclerite size has been documented for shallow water octocorals (Prada et al., 2008). Relating traits to environmental conditions and performance as mentioned in the introduction will help gain insight into population dynamics and give predictive power on how communities can change under global warming (McGill et al., 2006), which can help advise management strategies such as VME designation. The knowledge we have of deep-sea

ecosystems is still scarce, and relating traits to environmental gradients is hypothetical. More in-depth knowledge is therefore needed. Gathering data coupling species functionality, environmental variables and traits should be a fruitful avenue of future research.

2.5. Conclusions

- Skeletal composition and sclerite shape and size have the potential to affect the biomechanical characteristics of octocorals, but other parameters need to be taken into account.
- Skeletal composition, which underlies axis type as trait, can be to a moderate degree related to the different bathymetrical ranges occupied by *D. meteor* and *V. flagellum* but taking into consideration the bathymetric distribution of other calcaxonians and holaxonians (Braga-Henriques et al., 2013; France, 1996) we can see that species belonging to both suborder have extensive bathymetric ranges. Axis type is not a labile trait, calcaxonian and holaxonian axis evolved once (France, 1996), but subtle differences in axis elemental composition could reveal mechanical differences. Calcium and Mg content can serve to estimate differences in stiffness, but other properties such as toughness and strength also mediate the biomechanical properties of materials and should be taken into account in more exhaustive analysis than the one presented.

- Sclerite shape is a conserved trait, but their function is not fully understood therefore their biomechanical relevance needs further exploration. Sclerite size and shape usefulness as a predictor for niche seems limited. In order to better define niches of octocorals more traits should be studied. Species interaction amongst which is competition can be influenced by the different traits (Kunstler et al., 2016; Lavergne et al., 2010; Weither et al., 1998). If the differences in skeleton composition and sclerite size and type confer advantages to one or the other species under the conditions occurring where the species coexist, the traits have the possibility to affect the interactions. Consequently, interactions between species will be discussed in Chapters 3 and 4. Nevertheless as mentioned above, thorough information coupling traits, functionality and environmental variables is needed.

Chapter 3: Prey responses and competition interactions between Atlantic Vulnerable Marine Ecosystems indicator species*Viminella flagellum* and *Dentomuricea meteor* from the Condor seamount

3.1. Introduction

This chapter will explore the interactions between to co-occurring species taking into consideration their different traits such as skeleton composition as explored in Chapter 2. More specifically competition interaction for food items under different flow regimes will be studied.

Coral gardens, because of their uniqueness, fragility, life history traits, structural complexity and functional significance, meet the criteria for VMEs as defined by (FAO,2009, 2016; UNGA, 2007), as further described in Chapter 1. Coral gardens are considered ecosystem-engineers because they provide structural complexity through their framework (Buhl-Mortensen and Mortensen; 2005; Buhl-Mortensen et al., 2010; Mortensen et al., 2015; Carvalho et al., 2014) and harbour a myriad of associated fauna such as fish and invertebrates (Cartes et al., 2013; Gomes-Pereira et al., 2017; Husebø et al., 2002; Pham et al., 2015; Porteiro et al., 2013). Other organisms rely on the substrate that CWCs provide (Bo et al., 2009, 2012, 2015; Carreiro-Silva et al., 2017; Deidun et al., 2015). Furthermore, as benthic suspension feeders, CWCs represent a direct link between the pelagic and the benthic food chain (Buhl-Mortensen et al., 2010; Gili et al., 2006; Hill et al., 2014; Rossi et al., 2017).

Albeit the importance and value of coral gardens has been made evident by the scientific community, little is known on how the different species comprising coral gardens interact with one another and the type of possible interactions they experience. Exploitative competition could be one of them. This particular interaction consists of a reduction in resource availability without direct interaction between the competitors (Kim and Lasker, 1997), specially related to food in an environment generally believed to be mostly oligotrophic (Danovaro et al., 2014; De Goeij et al., 2013; Druffel et al., 1999). However, this depends on the seasonality and other aspects that remain knowledge gaps, or studied for specific systems (e:g Soetaert et al., 2016). According to the theory of competitive exclusion (Gause, 1934) *n* species cannot coexist on fewer than *n* resources, e.g. , if they share the same niche. But other views have explored the possibility of stable co-existences (Chesson, 2000; Vance, 1985), which depends on the competitive ability and fitness inequalities of the species considered (Chesson, 2000; Neil et al., 2009) defined by several parameters such as growth and death rates. Equally in order to coexcist intraspecific competition must be greater than interspecific competition (Chesson, 2000).

Co-existence also requires that species react differently to ecological heterogeneities such as different flow regimes (Leibold and McPeek, 2006). Coral gardens and CWC reefs generally rely on adequate food supply (Hebbeln et al., 2014), and being suspension feeders, they rely on seston supplied to their feeding apparatus (Patterson, 1991; Sebens et al., 1997; Ribes et al., 1999). Some mechanisms delivering food are strong bottom currents; downwelling, cascading;

internal tides and waves; and nepheloid layers, which act as a pathway for lateral transport to CWC-rich areas (Davies et al., 2009; Dorschel et al., 2007; Duineveld et al., 2004, 2007; Mienis et al., 2007; Orejas et al., 2009, White et al., 2005). Flow speed and direction characterise these flow regimes and can affect how efficiently corals feed (Sebens et al., 2017).

Different coral morphologies and traits, either whole colony or polyp morphology, affect how these organisms react to different flow regimes and the flow characteristics as explored in Chapter 2 and how effective they are capturing prey (Sebens et al., 1997). Concave coral shapes have been attributed to corals experiencing unidirectional flows because it confers advantages in minimising drag forces and catching prey items (Leversee, 1976; Grigg, 1972; Mortensen and Buhl-Mortensen, 2005; Theodor, 1963). Bushy or whip-shaped corals are believed to be adapted to turbulent and multidirectional flow (Mortensen and Buhl-Mortensen, 2005; Sebens et al., 1997; Theodor, 1963) and, last but not least, fan-shaped corals are suggested to be adapted to environments where bidirectional flow is present. Structural complexity has also been documented to be an adaptation to different flow regimes. Paz-Garcia et al. (2015) documented that the morphology of three scleractinian corals was consistently bushier and more densely packed in high flow environments. Similarly, Sebens et al. (1997) showed that densely branched colonies of the shallow tropical scleractinian *Madracis mirabilis* were more efficient at feeding at high flow speeds than sparsely branched colonies.

Polyp morphology, perhaps at a smaller scale, also determines how the organism reacts to flow regimes and how it impacts its feeding abilities. Bigger polyps are more easily deformed under high flow regimes compared to small polyps (Leversee, 1976; Porter, 1976), deformed polyps will impair feeding ability (Sponaugle and LaBarbera, 1991). On the other hand, at medium velocities, polyps reduce mainstream velocities creating eddies behind them that facilitate prey capture (Sponaugle, 1991). Bigger individuals of the anemone *Metridium senile* were more efficient at catching prey under low flow speeds, and medium and smaller individuals showed a higher efficiency at medium flow (Anthony, 1997). Polyp morphology tentacle size and nematocyst density also determine to some extent the particle sizes that corals are suited to feed upon (Lasker, 1981; Sebens and Koehl, 1984). Pinnules, a characteristic of octocorals polyp morphology, increase surface area, probably aiding in the capture of particles in the size range of phytoplankton to very small zooplankton (Sebens, 1984; Sebens et al., 2017).

Given the importance of food for sessile organisms such as octocorals, the idea that different species forming coral gardens could experience exploitative competition for food resources arises, leading to possible competitive exclusion through which one species outcompetes another (Hardin, 1960). Since flow regimes can affect feeding behaviour and efficiency (e.g. Orejas et al., 2016; Purser et al., 2010), and flow is predicted to change as a consequence of global change (Thornalley et al., 2018; van Gennip et al., 2017), would flow speeds affect competition relations by affecting species fitness and competitive ability and, potentially, their niches? However, little is known about how the circulation of

shelf seas might change under future climatic conditions in the local scale, Holt et al. (2018) predicted specific changes for the North Sea, majority of the currents show a decrease.

Coral gardens composed of two octocoral species *Dentomuricea meteor* and *Viminella flagellum* are common in the Condor seamount (Figure 3.1) (Tempera et al., 2012). These two octocorals have two different morphologies, *V. flagellum* is whip-shaped and has big polyps, whereas *D. meteor* is fan-shaped and has small polyps (Figure 3.1). Hence, they are good test organisms in order to understand how and if co-occurring octocorals compete for food resources, if this interaction is affected by different flow speeds, and if the different morphologies influence their competing abilities. In this study, these two model organisms were exposed individually and co-occurring to two different flow regimes. The corals were given isotopically labelled food to test whether feeding efficiency is affected by the presence of another species and different flow speeds. Incorporation of isotopic tracers (^{13}C and ^{15}N) was taken as a proxy for feeding efficiency.

3.1.1. Aims

This study aims to answer the following questions:

(i) Do different species feed more efficiently and/or incorporate more tracer under high flow conditions?

(ii) Can one species outcompete the other?

(iii) Do different flow speeds affect competitive interactions between *V. flagellum* and *D. meteor*?

The results of the present study could help understand in greater depth the importance of species interactions and how it could affect ecosystem functioning by improving our understanding of species and species-environment interactions, which in turn could modify important aspects such as nutrient cycling, for example carbon fixation.

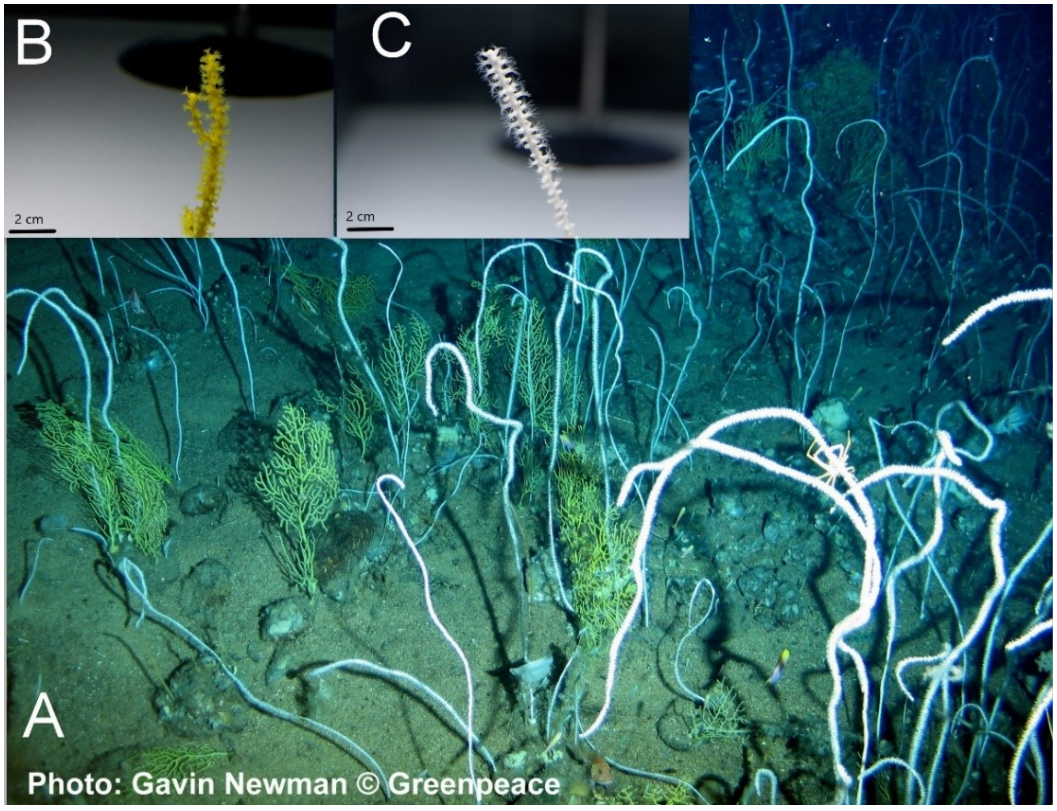


Figure 3.1. (A): Mixed species coral gardens from the Condor seamount, *Viminella flagellum* is the whip coral and *Dentomuricea meteor* is the yellow fan-shaped coral. (B): Experimental fragment of *D. meteor*, the polyps are observable. (C): Experimental fragment of *V. flagellum* were the polyps are observable. The scale bar is not exact, and should just be used for illustrative purposes.

3.2. Materials and methods

3.2.1. Specimen collection and maintenance

Viminella flagellum and *D. meteor* specimens were collected from the Condor seamount (38˚08'N, 29°05'W) (Figure 3.2) on the 28/11/2017 as bycatch from scientific longline fishing cruises (ARQDAÇO monitoring programme, University of the Azores), at depths ranging from 179 to 384 m on board the RV *Arquipelago*. After collection, colonies were transported to the DeepSeaLab Facilities at IMAR /DOP where they were fragmented into nubbins of 5 to 10 cm height and placed into putty epoxy support bases. The nubbins were placed into 35 l aquaria with a flow of 12 l h^{-1} the aquaria were placed in a water bath kept at contant temperature. The seawater supplied to the aquaria was from the bay in Horta, Azores (38°58'N; 28°78'W). The seawater was UV-light treated (Vecton 600, Tropical Marine Centre™) and filtered through a strainer filter bag (50 µm, Tropical Marine Centre ™). Aquaria were kept at a mean temperature of 14°C. Corals were fed daily with a mixture of frozen adult and *nauplii* of *Artemia,* mysids and microplakton. The specimens remained in these conditions for acclimation until used in the experiments.

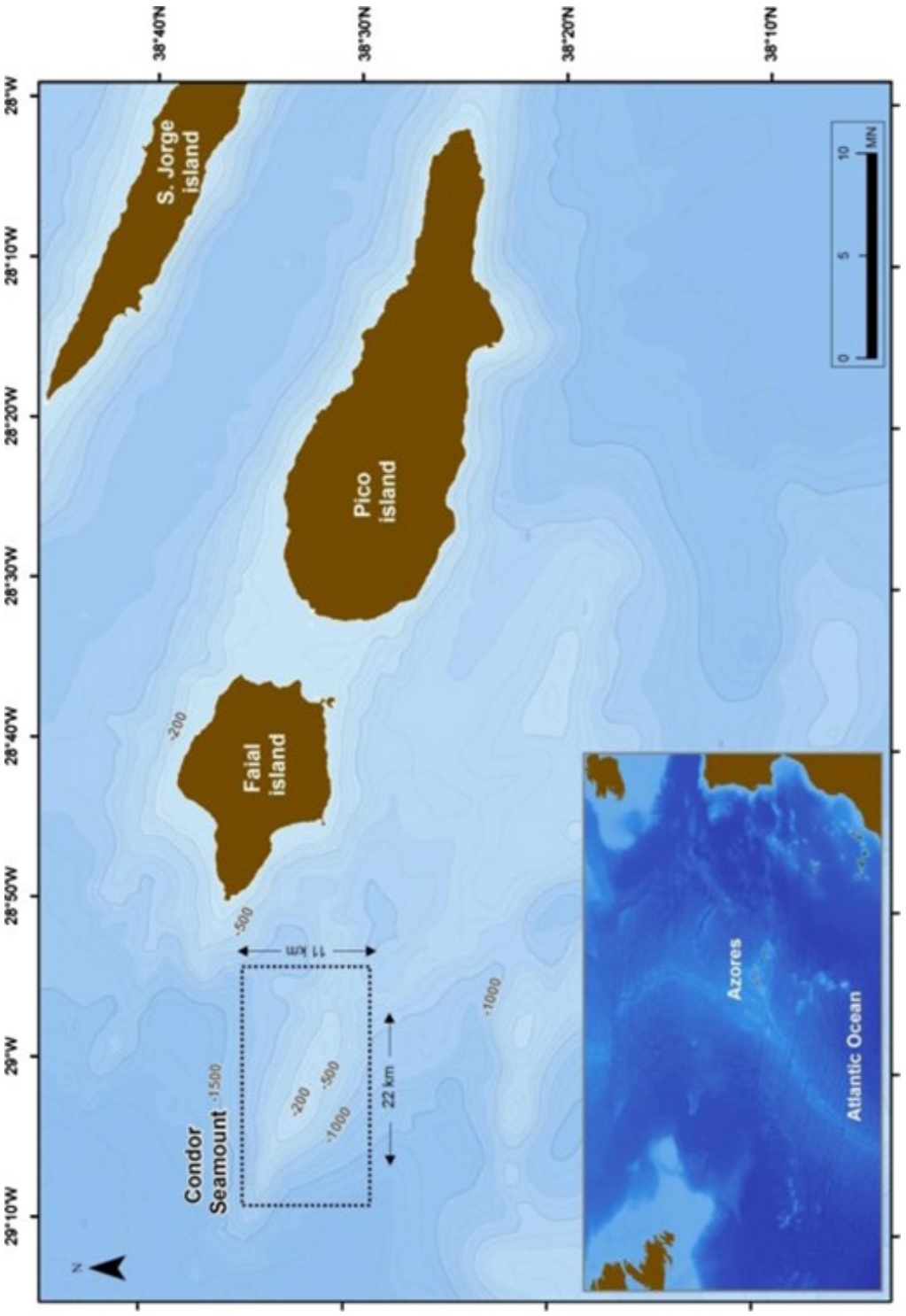


Figure 3.2: Condor seamount with the marine protected area delineated (dashed border). Taken from Ressurreição and Giacomello (2013) © Elsevier.

3.2.2. Isotopically labelled food production

Nannochloropsis microalgae were cultivated in artificial sea water enriched with f/2 media where 100% of the $NaHCO_3$ was replaced by 99% $NaH^{13}CO_3$ (Sigma-Aldrich) and 50% of the $NaNO_3$ by 99% $Na^{15}NO_3$ (Sigma-Aldrich). Each litre of culture media consisted of 800 ml of artificial sea water and 200 ml of natural sea water filtered through a Gf/F filter (WHATMAN). The algal cultures were cultivated for 3 weeks at a temperature of 14°C and a light cycle of 16 h light and 8 h dark. The algal cells were harvested at a mean concentration of $2.9*10^7$ cells ml^{-1} (a total of 54 l of algal culture were produced).

Stock cultures of the rotifer *Branchionus plicatilis* at a concentration of 87 individuals ml^{-1} were fed isotopically labelled algae. Each 12 l stock culture was fed twice daily for 4 days with 0.8 l of isotopically labelled micro algae suspension at a concentration of $2.9*10^7$ cells ml^{-1}. After the incubation time, *B. plicantilis* cultures were separated into equal portions of 500 ml aliquots, filtered through 41 µm mesh, rinsed with filtered seawater packed into plastic containers and frozen at -18 °C until used. Samples of *Nannochloropsis Branchionus plicatilis* were analysed for isotopic composition , procedure is describe in the section 3.2.4

3.2.3. Experimental design

To assess competition under different flow regimes, one specimen of each species was placed together at the same distance upstream of the flow on a 35 l flume (Figure 3.3) placed in a water bath. Two water speeds were tested: 4 cm s^{-1} and 2 cm s^{-1}, these flow speeds were chosen because they are known to occur in the Condor seamount (Bashmachnikov et al., 2013). Four experimental replicates

of each treatment were performed. After the nubbins were transferred to the experimental flume, they were left to acclimate for 24 h with a flow of 12 l h^{-1}, before the experiments commenced. After the acclimation period, the propellers attached to a rotating 12 V engine (SERVOCITY) were introduced to the flumes to create laminar water flow currents at the desired speeds of 2 and 4 cm s^{-1}, and corals were left to acclimate to the water speeds for 1h. Following this, the flow through system was closed and the previously thawed isotopically labelled rotifers, were added to each flume. Food incubations lasted for 12 hours, pH and temperature were measured at the beginning and end of the incubation period, pH and temperature dropped on average 0.065 ± 0.03 units and 1.14 ±0.17° C, respectively, for all aquaria. The temperature in the flumes decrease despite being placed in temperature controlled water bath. Subsequently, 5 l water samples were taken, propellers were removed, water intake was opened and the flume was siphoned to remove food residuals. Water samples were filtered through Gf/F filters dried at 60 °C for 24 h, weighed, then burned at 450 °C for 4 h and re-weighed to assess the amount of carbon left in the water. This process was repeated for 6 consecutive days, with 12 hours intervals in between each food incubation period. Between each incubation period 5 l samples were collected from each flume, samples were filtered through a Gf/F filter dried at 60° C for 24 h, weighed then burned at 450 °C for 4 h and re-weighed, to estimate the background amount of C present in the seawater. As a control treatment for competition for food resources, each species was tested individually by placing a single individual in the flume and expose it to the 2 different water speeds. Control

2 cm s^{-1} and Control 4 cm s^{-1} were the control treatments for each species. The same process as described above was performed for the control treatments, with each control treatment having 4 replicates in total. Only four flumes were available hence the experiments had to be performed in batches.

3.2.4. Sample processing

After the six incubation periods were finished for each batch, the specimens were collected and frozen at -18 °C one hour after the end of the feeding incubation, thus loses due to respiration were considered minimal.. When all the experimental batches were finished all the samples were freeze-dried and weighed to obtain Dry Weight (DW). The dry samples were then shipped to the University of Edinburgh.

Coral tissue was separated from the skeleton, weighed; and homogenised with a pestle and mortar. For ^{13}C analysis, aliquots of 4 mg of each sample were weighed into silver capsules and were subsequently acidified stepwise with 5% HCl to eliminate inorganic carbon. The acidification process was repeated until no bubbling was observed. The samples were dried over night at 50 °C between acidification episodes. For ^{15}N analyses 2 mg of each sample was weighed in tin capsules. All samples were analysed for isotopic ratio using EA-IRMS (Elemental Analysis Isotopic Ratio Mass Spectrometer) HS20-22E (SERCON). Stable isotope data are presented as a per thousand (‰) deviation from a standard as δX (‰) = ((R sample – R reference)-1) x 1000, where (X) is ^{13}C or ^{15}N, R sample is the isotope ratio ($^{13}C/^{12}C$ or $^{15}N/^{14}N$, respectively) in the sample and R reference is the isotope ratio of the reference materials. These references are materials that have been

selected and assigned definitive delta (δ) values for the light elements by the International Atomic Energy Authority. For C, R reference = 0.0111797 was taken from Pee Dee Belemnite and was based on a Cretaceous marine fossil, *Belemnitella americana.* For N, R reference = 0.0036765 was taken from air. The atomic fraction (F) of ^{13}C and ^{15}N in specimens was calculated with F=R/(R+1). Excess values (E) are calculated as E = F sample–F background, so that positive excess values indicate uptake of the isotopically-labelled food. Total ^{13}C and ^{15}N assimilation was calculated as the product of excess (E) and the biomass of the specimen (Moodley et al., 2005). The biomass was expressed in C and N units and calculated by multiplying the specimen's DW with C and N content (as % of specimen's DW). The normalisation of total C and total N assimilation to specimen's biomass was carried out through the division of total C and total N assimilation by biomass (in C or N units, respectively). The total amount of tracer incorporated from the food source into each fragment (tracer C incorporation, µmol tracer fragment^{-1}) was calculated by dividing each ^{13}C assimilation by the fractional abundance (F13 and F15) of the labelled food normalised, C and N incorporation was expressed as [µmol tracer (mmol OC)$^{-1}$]. The calculations were done for each of the four replicates for the two treatments and the two controls.

3.2.5. Statistical analysis

Data was analysed using the statistical software R version 3.5.1 (R Core Team, 2018). Assimilation of ^{13}C and ^{15}N values did not have a normal distribution therefore Kruskal-Wallis non-parametric test was used to analyse the data.

Kruskal-Wallis Multiple comparison test between treatments or treatments versus control were done using R package pgirmess (Giraudoux et al., 2018).

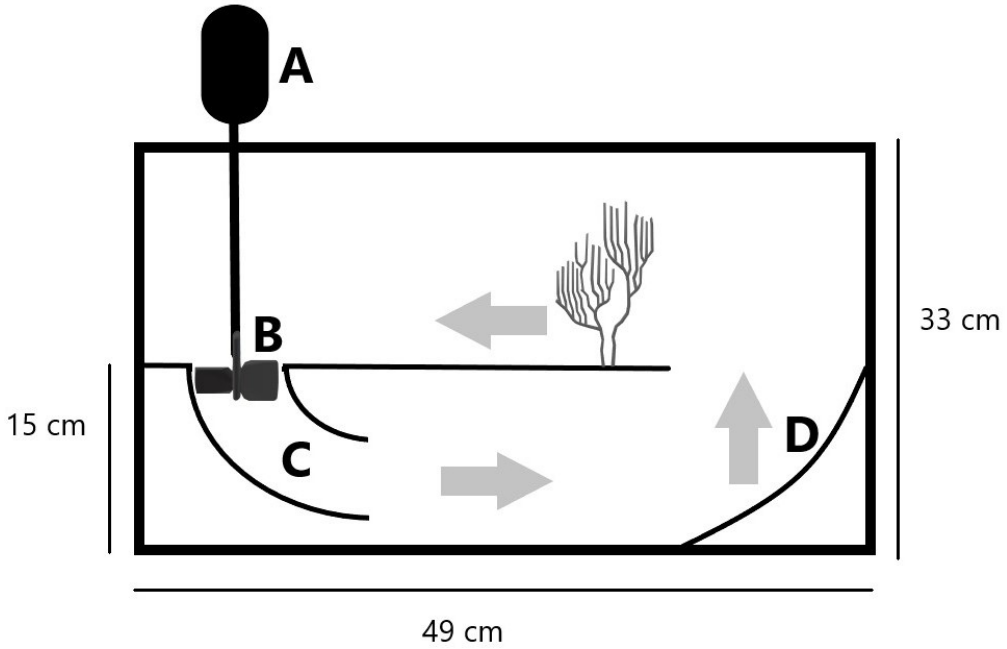


Figure 3.3: Schematic representation of the experimental 35 l flume used, width was 20.4 cm. (A): 313 rpm motor; (B): 8 cm propeller; (C): tube facilitating the creation of laminar flow; (D): ramp to decrease localized water turbulence. Arrows indicate flow direction.

3.3. Results

All the tested corals incorporated tracer into their bulk tissue (Table 3.1). Data suggested that both species incorporated more tracer and so fed more efficiently under high flow.

Fragments of *D. meteor* under higher speed displayed the highest incorporation rate for this species (Figure 3.4 A and B, Table 3.1) under control and competition conditions. However, no statistical differences were found (Figure 3.4 A and B, Table 3.1), but trends were identified. Under low speed condition (2 cm s^{-1}), tracer incorporation was slightly higher under control treatment than under competition conditions. However, under high flow conditions the incorporation rate for *D. meteo*r was higher when in competition. *Viminella flagellum* also incorporated more ^{13}C and ^{15}N tracer at high speeds (4 cm s^{-1}), either when in competition or in control treatments. Under both flow treatments *V. flagellum* exhibited a higher incorporation rate when in competition than in control. The observed differences were not statistically significant (Figure 3.4 C and D, Table 3.1).

Competition experiments revealed that *D. meteor* has higher incorporation of both ^{13}C and ^{15}N tracers than *V. flagellum* under both flow speeds, this difference was significant just for high speed treatment (4 cm s^{-1}) (p-value: 0.02), (Figure 3.5, Table 3.1). Control treatments showed no significant differences between species, most likely due to the observed high variation.

Table 3.1: Average ^{13}C and ^{15}N bulk tracer incorporation in *V. flagellum* and *D. meteor* for each treatment (2 and 4 cm s^{-1}) and the respective controls.

Species /treatment		**C tracer incorporation [µmol C (mmol OC)$^{-1}$]**	**N Tracer incorporation [µmol N(mmol N)$^{-1}$]**
V. flagellum	Control 2 cm s^{-1}	5.57 ± 4.49	5.16 ± 3.96
	Experimental with *D. meteor* 2 cm s^{-1}	12.74 ± 12.46	10.44 ± 9.63
	Control 4 cm s^{-1}	8.32 ± 8.57	8.69 ± 8.69
	Experimental with *D. meteor* 4 cm s^{-1}	12.24 ± 8.01	14.53 ± 9.92
D. meteor	Control 2 cm s^{-1}	26± 24.39	19.21 ± 19.41
	Experimental with *V. flagellum* 2 cm s^{-1}	18.25 ± 14	17.84 ± 8.9
	Control 4 cm s^{-1}	28.48 ± 15.69	28.23 ± 20.56
	Experimental with *V. flagellum* 4 cm s^{-1}	68.89 ± 53.83	65.94 ± 38.13

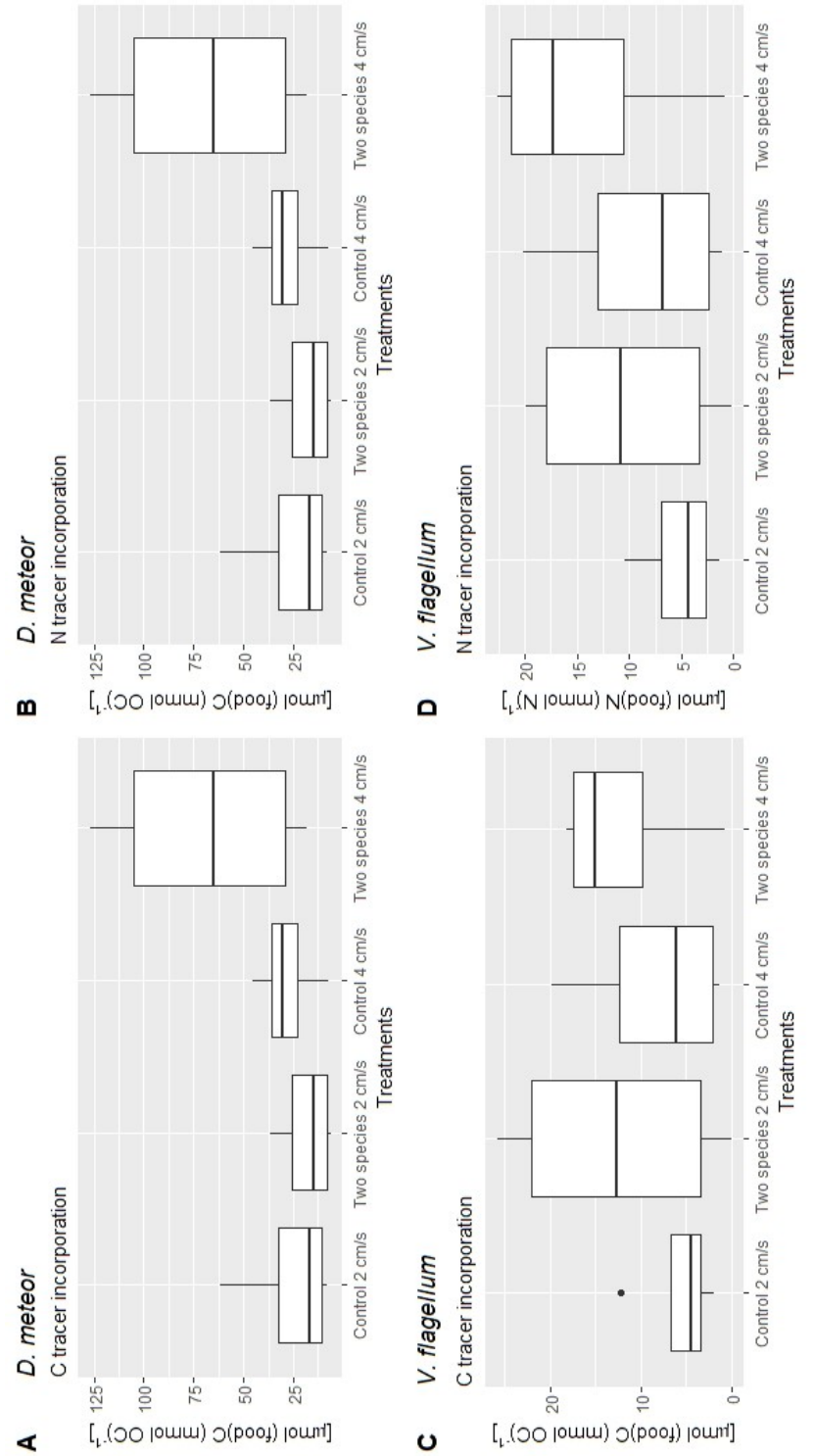


Figure 3.4: Average tracer incorporation for the octocorals under the speed treatments 2 and 4 cm s^{-1}, two species together and Control single species. (A): *Dentomuricea meteor* ^{13}C incorporation. (B*): D. meteor* ^{15}N incorporation. (C): *Viminella flagellum* ^{13}C incorporation. (D): *V. flagellum* ^{15}N incorporation. Note the different scales in the y axes. Black dots represent outliers.

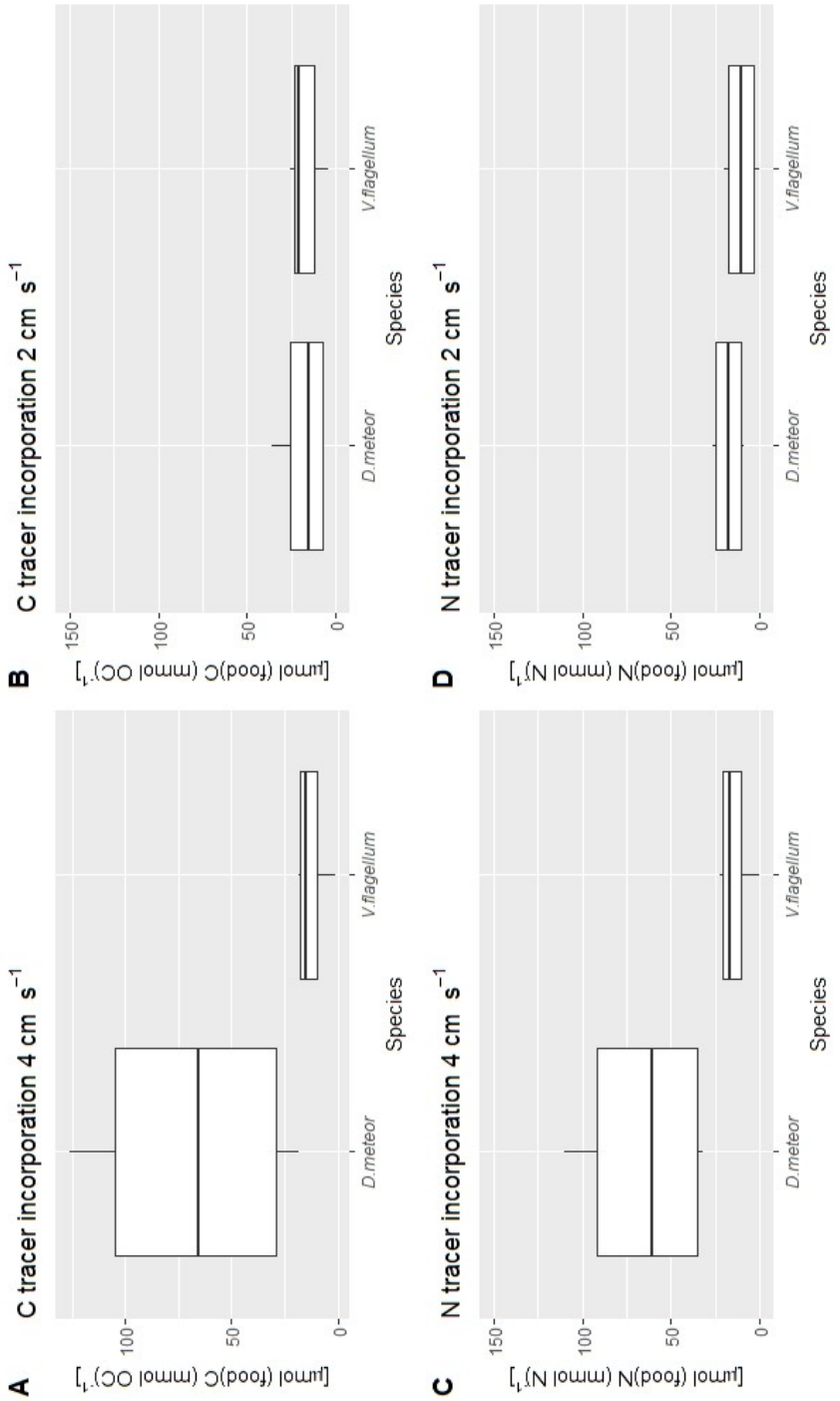


Figure 3.5: Average tracer incorporation for the octocorals under competition conditions (both species together). (A): ^{13}C incorporation under 2 cm s^{-1}. (B): ^{13}C incorporation under 4 cm s^{-1}. (C): ^{15}N incorporation under 2 cm s^{-1}. (D): ^{15}N incorporation under 4 cm s^{-1}.

3.4. Discussion

3.4.1. Speed effect on feeding efficiency

Both species showed higher incorporation rates of both tracers at 4 cm s^{-1} most likely due to higher prey encounter rate per unit of time (Sebens et al., 1998). Conversely, flow speed at 2 cm s^{-1} may have not been sufficient to keep enough food in suspension and the lower speed will also represent a a lowe prey encounter rate (Sebens et al., 1998). Moreover, at the measured low speed, the force with which the food items impacted the tentacles may also have not been enough to induce a nematocyst response, as seen for other species (McFadden, 1986). The minimum speed found by McFadden (1986) was 0.04 m s^{-1}, but this might have been species-specific. Several other aspects of food particles properties have not been taken into account when assessing particle capture in suspension feeders. For example, denser large particles such as the rotifers used in my study could be more easily caught under high flow regimes due to inertial impaction, meaning that because of their density, particles deviate from the streamlines and contact the feeding apparatus of the suspension feeders (Sebens et al., 1998).

3.4.2. Competition between species and the effects of flow on it

Dentomuricea meteor had a higher incorporation rate of both tracers for all treatments when compared to *V. flagellum*, which suggest that the former has the possibility to catch more food per unit of time and potentially have more chances to outcompete *V. flagellum.* This hints to niche overlap and potential exclusive competition, which could be even more probable under higher flow conditions since the incorporation of tracers was significantly three times higher

under high flow. The variability of the results is typical of the deep sea, and all live organisms, and despite the observed variability of the data, the differences under the high speed treatment were still significant. However, in order to assess the possibility of exclusive competition, other parameters should be taken into account such as morphological differences and changing hydrodynamic conditions (for a further discussion see below).Equally to properly determine the existence of exclusive competition the amount and quality of food has to be quantified, since exclusive competition occurs when resources are limited (Gause 1934). In addition, as already observed for other deep-sea corals, flow speed can affect the type of prey corals preferentially feed on (Orejas et al., 2016). The Condor seamount presents a dynamic system (Bashmachnikov et al., 2013) where flow and current speeds change throughout the year spanning approximately from to 13.5 cm s^{-1} in May to 1.5 cm s^{-1} in October (for further detail, the reader is refered to figure 2 Bashmachnikov et al., 2013) prey diversity varies seasonally as well (Carmo et al., 2013; Santos et al.,2013). These variations can create separate temporal niches that *V. flagellum* and *D. meteor* could exploit and feed readily when the current regime enables them to, according to their distinct traits. Conversely, in the present study, the higher incorporation rates for ^{15}N and ^{13}C for both species under competition conditions hints that the flow modulation by several species, or several individuals in the same aquaria has a positive effect in feeding. Due to shortage in specimens, the controls could only be done with one individual per aquaria. It would be interesting to see if similar results are observed when tested alongside conspecifics.

The fact that these species are found in co-existence prompts the exploration of other possible relationships. For example, the concept of facilitating cascade. *V. flagellum* and *D. meteor* could be idealised as foundation species (synonym for bioengineer) where *D. meteor* facilitates for *V. flagellum* by reducing water flow speed. Facilitating relationships of two similar species are usually observed when one of the species is in the edge of its tolerance limit (Chesson, 2000). Here, I propose that when *V. flagellum* and *D. meteor* are found in mixed gardens, the former is close to the tolerance limit for flow speed, but is enabled to thrive because of the presence of *D. meteor*. This argument is further reinforced when the natural distribution of the two species is taken into account. The monospecific gardens of *V. flagellum* have been associated to moderate to low flows in the Mediterranean and in the Condor seamount, where the species shows a preference for steep slopes (Cau et al., 2015, 2017; Giusti et al., 2012, 2017; Porteiro et al., 2013). *Viminella flagellum* is also found forming monospecific gardens in the Northern flank of the Condor seamount were current speeds are lower (0.6 and 2.6 cm s^{-1}) compared to the summit (2 to 6 cm s^{-1}). The preference of *D: meteor* for higher flow can possibly be explained due to its higher metabolic rate (Rakka et al.,in preparation) which could just be met in high-flow, high-food conditions, whereas *V. flagellum* can also occur in low- flow and low-food environments because it has a lower metabolic rate.

The bigger polyps presented by *V. flagellum* correspond with its habitat preferences. Big polyps are also advantageous when living in higher sedimentation habitats (Prada et al., 2008), which can be characteristic of low to moderate flow

areas. Quattrini et al. (2017) found that deeper dwelling octocorals of certain taxonomic groups tended to have bigger polyps than their shallower counterparts. This supports the fact that *V. flagellum* has a more extensive depth range than *D. meteor* (Braga-Henriques et al., 2011, 2013, Tempera et al., 2011) and perhaps is better adapted to dwell in deeper depths than *D. meteor* as already discussed in Chapter 2 according to skeleton and sclerite trait differences. However, polyp size can be interpreted in different ways, small polyps of *Leptogorgia sarmentosa* have been documented to feed efficiently in plankton bettween 80–200 μm (Rossi et al., 2004) , suggesting that the small polyps could also be advantageous to feed on smaller food particles found in depleeted and low flow areas.

On the other hand, *D. meteor* in the Condor seamount has been found preferentially in the summit, either in mixed or monospecific gardens (Braga-Henriques et al., 2011, 2013; Tempera et al., 2011), where currents are stronger (Bashmachnikov et al., 2013; Genin, 1986). It has been postulated that the distribution of co-existent species is not haphazard (Gili and Coma, 1998), and that different coral species can self-arrange to maximize food acquisition reinforcing a possible facilitating cascade. Assessing this with long-lived benthic animals can be complicated because the process might have happened over very long periods (Gili and Coma, 1998). Spatial distribution of species in coral gardens has not been examined and could potentially give us insight into their ecology, and how they mediate co-existence.

The findings of this study suggest, as already mentioned, that *D. meteor* is more efficient at catching the given food item, but the energetic needs of the two different species have not been taken into consideration. The fact that *V. flagellum* catches less food does not mean that it can be outcompeted, especially if it might have a lower basal metabolic rate than *D. meteor*. Rakka et al. (in preparation) documented a lower respiration rate for *V. flagellum* than for *D. meteor,* 0.151 ± 0.036 0.308 ± 0.042 µmol O_2 mmol tissue C^{-1} h^{-1} respectively. In Chapter 2 it was made evident that the skeleton of *V. flagellum* is made of 30 % calcitic material while *D. meteor* is less than 1% calcite. According to Mistri (1996), the energetic cost of laying down an inorganic skeleton is lower than that for a proteinaceous one, hence it could be theorised that *D. meteor* uses more energy to lay its skeleton when compared to *V. flagellum*.

3.4.3. Morphology and other traits, and aspects possibly affecting competition

Higher food uptake by *D. meteor* can be due to it being a branching/fan-shaped coral, which can create eddy turbulence around the branches increasing the possibility of prey encounter. Patterson (1984) documented the importance of eddies for downstream polyps to catch prey in the octocoral *Alcyonium siderium* when they were exposed to laminar flow, as was done in the present study. Other studies have also shown the importance of eddy formation under higher flow speeds for corals to catch prey (e.g. scleractinians, Helmuth and Sebens, 1993; Sebens et al., 1997; Wijgerde et al., 2012). At the polyp level, Spongaule (1991) also described the same phenomena. As explored in Chapter 2, skeleton composition and biomechanical characteristics such as stiffness, affect the

performance of the corals in the water column, hence they might also affect their feeding strategy.

Contrasting polyp morphologies can also explain the differences in feeding efficiencies between the two species when they occur in mixed gardens, as suggested by the present results. *Viminella flagellum* has larger and longer polyps than *D. meteor*. These larger polyps become more deformed at increasing velocities (Anthony, 1997). This can reduce the speed range at which this species is more effective at catching prey, compared to the range of corals having smaller polyps (Chang-Feng and Ming-Chao, 1993), such as *D. meteor*. As Chang Feng and Ming Chao (1993) observed when comparing feeding abilities for three octocorals under varying flow conditions, the coral having a narrower flow speed feeding range presented a higher feeding efficiency at a specific flow speed. The opposite trend has been observed in deep-sea scleractinians, *Dendrophyllia cornigera* having polyps ranging from 2 to 4 cm fed efficiently at a wide range of flow speed when compaires to *L. pertusa* which feeds more efficiently at lower speeds (Gori et al., 2015; Purser et al., 2010). Suggesting that the flow range at wich corals are efficient at feeding can be taxon specific and is dependent on more factors than just polyp size.

The findings of this study suggest that *V. flagellum* in competition under both flow speeds has a higher assimilation rate when compared to the respective controls, which perhaps can be explained also by the fact that two organisms in

one aquarium create more eddy turbulence in the water flow, increasing particle encounter with the polyps.

Other aspects of polyp morphology such as pinnules spacing and length can explain the differences in feeding efficiency of the tested octocorals. These characteristics can confer advantages when handling different types of prey (Sebens et al., 1998), as hypothesised for two different azooxanthellate octocorals of the Red Sea *Dendronephthya hemprichi* and *Dendronephthya sinaiensis* (Grossovicz and Benahayu, 2012). Ribes et al. (2003) also hypothesised that higher capture rates of the Mediterranean species *Leptogorgia sarmentosa* when compared to *Paramuricea clavata* could be possibly explained due to differences in pinnules and tentacle spacing, the latter species having smaller spacing between pinnules could have an advantage when capturing and handling small prey. Due to equipment constrains, we could not measure pinnule density and size of the two tested species, but it is an aspect worthwhile exploring.

Nematocyst density has also been hypothesised to affect prey capture and handling efficiency in octocorals and hexacorals (Mariscal and Bigger, 1977). Higher density of nematocysts can provide the corals with a better chance of catching motile prey (Lasker, 1981). Due to the low nematocyst density in octocorals compared with hexacorals (Mariscal and Bigger, 1977) several authors have hypothesised that octocorals feed preferentially in low motile prey (Ribes et al., 2003).

Quattrini et al. (2017) observed higher variability in the morphological traits found in deep-sea octocorals observed in shallower depths (250 to 800 m) compared to octocorals found deeper in the seafloor, prompting the suggestion that different species may specialise on different food particle sizes, and this could lead to local coexistence of numerous species at shallower sites. The different morphological characteristics and traits warrant further investigation to better understand the differences in feeding efficiency of *V. flagellum* and *D. meteor*.

The morphological differences of the two studied species could possibly represent strategies to partition resources, allowing the different species to exploit different food sources or similar ones at varying heights of the water column. For example, *V. flagellum* rises higher up in the water column, hence, it most likely gets access first to food items in the water column, akin to the fact that different tree species using the same resources have different root lengths in order to avoid competition (HilleRissLambers et al., 2012; Shiffers et al., 2011). The larger polyps of *V. flagellum* could possibly enable to feed on bigger prey items.

The present study assessed competition based on one food source, which was the preferred experimental food source for both of the species (Rakka et al., in preparation). However, different zooplankton and other food sources might be available reducing competition for a single food resource. The Condor seamount presents highly variable hydrodynamic regime (Amorim et al., 2017; Bashmachnikov et al., 2013), which could translate into variations in the zooplankton assemblages that reach the corals gardens. Throughout the year,

zooplankton biodiversity varies, Carmo et al. (2013) studied zooplankton abundance and diversity in the Condor seamount during the months of March, July and September. Appendicularia and Doliolida had higher abundances exclusively in summer while Calanoida had higher abundances in spring and autumn. This variability presents different prey items for the corals. Other possible food source is phytoplankton material and, according to Santos et al. (2013), this resource also varies with season, in regards to amount and species composition. Phytoplankton reaches deeper in the water column during summer months making it more readily available to benthic consumers such as octocorals. Detrital matter should also be considered as an important food source for the benthic communities, given their heterogeneous nature (Beaulieu, 2002; Campanyà-Llovet et al., 2017) and therefore providing different possible prey items for the corals. Particulate organic matter concentrations reaching the Condor seamount vary seasonally from 180 µmol m^{-2} d^{-1} in winter to 1600 µmol m^{-2} d^{-1} in late spring (Wolff et al., 2019).

The conditions on the Condor seamount do not seem to be food limited, especially taking into account food variety.

However if both species were dependent on the exact same resource or resources were limited it could cause competition and competitive exclusion, thus selectively preying on different zooplankton, phytoplankton or detrital material can be a possible explanation on how these two species co-exist in mixed coral gardens, which can be mediated by the above mentioned morphological

differences by resource partitioning, which is considered a stabilising mechanism that can be defined as effects increasing intraspecific competition relative to interspecific (Chesson, 2000).

Historically, the niche has been defined as having various axes: temporal, spatial among others (Hutchinson, 1957). The possible different food sources represent distinct niches, and the varying availability of food sources represent different temporal niches. Similarly, the fact that the two species can occupy different heights on the water column can also represent separate spatial niches that the species are able to exploit.

Before properly talking about exclusive competition because of food resources, better characterisation of the respective prey items of the two species should be done. Overall species average fitness, defined as a summary ability of the species to succeed in the given environment relative to other species in the same guild (Chesson, 2018) should also be taken into account when assessing species competition and coexistence. The more dissimilar the average fitness is, the less likely species are able to co-exist if their niche does not differ sufficiently (Chesson, 2000). But very little information, if at all, is known about the two studied species. In laboratory conditions, *D. meteor* is more sensitive and has higher mortality rates than *V. flagellum* (personal observation). If this observation holds true in the natural environment, it could mean than the latter species has a higher value for the survival fitness component. This emphasises the importance

of understanding different aspects of the ecology of co-existing species before assessing possible exclusive competition.

3.5. Conclusions

- Although the observed differences were not significant, the results suggest that at the tested high speed (4 cm s^{-1}) both *V. flagellum* and *D. meteor* incorporated more ^{13}C and ^{15}N tracer into their tissues meaning that the two octocorals were more efficient at catching prey items at the tested higher speeds.
- *Dentomuricea meteor* exhibited higher incorporation of tracer in both treatments suggesting it has the capacity of outcompeting *V. flagellum* albeit this difference was just significant under high speed treatment. Nevertheless, the present study was limited, and other relationships between the two species might be into play, for example a facilitation interaction. Equally global change could also change the dynamics of the two species, their tolerance to higher temperatures and acidified conditions should also be investigated.
- Taking into consideration the results of this study, niche overlap regarding food resources can be suggested. Factors such as the morphological, ecological differences, the possible different prey available, and the changing hydrodynamic conditions should be investigated before assessing competitive exclusion and other interactions.
- If abiotic forcing changes the dynamics of coral gardens, it could represent in the long term a decrease in biodiversity. Species that partition food

resources represent a more efficient exploitation of the food reaching the seafloor (Cardinale et al., 2006), meaning more nutrient fixation. Hence changes in biodiversity will affect nutrient re-cycling (Cardinale et al 2012). Changes in biodiversity could be first observed as changes in the population dynamics between *V. flag*ellum and *D. meteor*, these changes are difficult to detect due to the longevity of CWCs (Snelgrove et al., 2014). Such modifications will bring shifts in the epibenthic communities associated to one or the other species, which could further exasperate nutrient cycling.

Chapter 4: Responses to different food types and feeding efficiency between passive and active feeders composing vulnerable marine ecosystems (coldwater corals, sponges and bivalves) from the Norwegian Shelf

4.1. Introduction

This chapter will explore the preference of different VME indicator taxa for different food particles based in size and type. The effect of flow in feeding efficiency and preferences will be evaluated.

As discussed in detail in Chapter 1, CWCs and sponges are important ecosystem engineers in the deep sea providing structural habitat complexity that can harbour many associated species (Beazley et al., 2013; Buhl-Mortensen et al., 2010; Kutti et al., 2013), enhance carbon deposition to the seafloor (Bell et al., 2008; Soetaert et al., 2016; van Oevelen et al., 2009), and contribute to the cycling of other key elements such as Si and N (Maldonado et al., 2012;Hoffman et al., 2009).

As benthic suspension feeders both CWCs and demosponges provide an important direct link between pelagic and benthic food chains (Buhl-Mortensen et al., 2010; Maldonado et al., 2012) mediated by different feeding strategies. Distinct feeding strategies are considered different traits. During active suspension feeding, sponges and bivalves actively pump water through their systems to capture food particles, while passive suspension feeders, such as corals, rely on water currents to transport food particles to their feeding structures. In sponges, water enters through pores called ostia and is pumped into an aquiferous channel

system by the flagella of specialised cells called choanocytes. The water is then filtered in the choanocyte chambers through a collar filter and released through an osculum, each fed by several ostia (Riisgård and Larssen, 2010). In contrast, bivalves use the ciliated surface of their gills to create currents that flow across the gills and mantle cavity, where the water is filtered. Bivalves possess different morphological features that are believed to aid in particle selection, such as the vellum (Ward and Shumway, 2004) and well-developed laterofrontal cilia that help capture small particles (Riisgård and Larssen, 2010). Reef framework-forming CWCs, such as *L. pertusa*, are passive suspension feeders that have typically been regarded as capturing food items from the water through physical contact with their nematocyst-laden tentacles and subsequent transfer by the tentacles into the actinopharynx and coelenteron where food is processed (Mortensen, 2001). However, it was recently shown that *L. pertusa* can also use mucus nets to catch prey (Murray et al., 2019).

Cold-water corals and sponge grounds are very vulnerable to the effects of changing climatic conditions (Danovaro et al., 2017, Levin and Le Bris, 2015; Roberts and Cairns, 2014; Roberts et al., 2016). Under IPCC scenario RCP 8.5 only 30% of deep-sea corals will be in $CaCO_3$ saturated waters in 2100 and by 2300 this declines to just 5% (Zheng and Cao, 2014). Food supply to the deep seafloor is also projected to decrease, which will cause decline in benthic biomass (Jones et al., 2014). Other changes in abiotic factors due to global change include oxygen concentration decrease, warming and changes in current patterns (see Chapter 1 for a summary). These changes will also diminish suitable habitats for CWCs.

Water temperature changes can also affect the water viscosity, which can affect the ability of suspension feeders of catching certain prey items (Vogel, 1994). Flow conditions and food availability are two aspects projected to be affected by climate change (Levin and Le Bris, 2015; Smith et al., 2008). Flow conditions on the world's ocean basins are projected to change, the most predominant feature of these changes is the slowing down of the AMOC , possibly because of excess input of fresh water from the Nordic seas and polar regions (Caesar et al., 2018; Thornalley et al., 2018). Changes in AMOC circulation will bring changes in other current systems (Frajka-Williams et al., 2019). Climate change will also intensify the frequency and intensity of extreme weather events (Knutson et al., 2010) with major implications for surface currents and sediment transport (Ulses et al., 2008). Several species have been documented to behave differently under varying flow regimes. For example, *L. pertusa* feeds more efficiently on zooplankton at low current speeds, and more efficiently on phytoplankton at higher speeds (Orejas et al., 2016). In contrast, the mussel *Mytilus edulis* presents filtration inhibition at high current speeds (Wildish and Miyares, 1990), while the scallop *Placopecten magellanicus* presents an optimum feeding velocity of 3 to 6 cm s^{-1}, but above this speed filtration is reduced (Wildish and Saulnier, 1993). There is also evidence that sponges have a behavioural response to increased ambient currents, reducing their pumping rate when exposed to very high ambient velocities (Ludeman et al., 2017).

Changes in ocean circulation may also cause changes in food supply, both vertical and horizontal food transport (Ulses et al., 2008). In the short term more

food can be available to the benthic communities, as documented for the Gulf of Lion (Rumín-Caparrós et al., 2013) and for the abyssal Northeast Pacific Ocean (Smith et al., 2013) translating into a shift to more opportunistic species. However, in the long term, global models predict an average decrease of export of Particulate Organic Carbon (POC) to the deep sea (Jones et al., 2014; Sweetman et al., 2017). This decrease is due to two processes: reduction of surface primary production, and enhanced water stratification, which directly limits food export (phytoplankton and zooplankton) from the surface to the deep sea. Thus, the quantity and quality of POC flux from the euphotic zone to the abyssal seafloor will be altered (Gregg et al., 2003; Smith et al., 2008). Currently, it is not clear how much of the decline of POC is due to surface reduced primary productivity or to enhanced water stratification. It is clear that increased water stratification also limits surface productivity (Bopp et al., 2001). Changing POC quality can have consequences for diversity in benthic ecosystems (Campanyà-Llovet et al., 2017).

The deep sea is generally recognised to be a food-limited ecosystem, but certain topographical features can enhance the food that reaches these environments (Genin et al., 1986; Soetaert et al., 2016). However, enhanced stratification and lower surface productivity, may negatively impact the energy balance of CWCs.

Reducing POC flux and quality may have serious consequences for biodiversity and ecosystem functioning (Jones et al., 2014; Smith et al., 2003, 2008). For instance, the distributions of *L. pertusa* and *Madrepora oculata* are strongly associated with increased surface primary productivity and high-energy

environments, including locally generated internal waves that rapidly supply labile food particles from the surface to the seabed (e.g. Davies et al., 2009; van Oevelen et al., 2009). Similarly, sponge grounds in the Canadian North Atlantic have been related to high internal wave activity, which is associated with increase food supply (Davison et al., 2019). Deep-sea bivalves are found in association with high food quality (Johnson et al., 2013) and are predicted to be impacted by changes in food supply (McClain et al., 2012). Hence it could be expected that organisms accustomed to low food availability would be able to exploit higher food inputs, which can come in natural environments as pulses.

Given the different feeding strategies shown by VME indicator species it is vital to understand their feeding ecology so that properly informed assessments can be made of their response to altered conditions and how it can affect their interactions. For example, passive suspension feeders could be expected to be more efficient in higher water flows since higher water speed will increase the probabilities of prey encounter with the filtering apparatus, i.e. higher particle flux (Lesser, 1994; Wildish and Kristmanson, 1997). However, studies have shown that intermediate speeds are preferred due to polyp deformation at high speeds (Orejas et al., 2016; Porter, 1976; Purser et al., 2010). On the contrary, active suspension feeders could be expected to be more efficient at lower flow speeds since they can actively pump water to extract food, thus being more dependent on food concentration (Gili and Coma 1998; Lesser, 1994).

Possible food competition relationships have been studied in shallow habitats by means of stable isotopic composition, the general results are that

different species feed on different subsets of the available seston evidenced by the differences in ^{13}C and ^{15}N tissue enrichment (Dubois and Colombo, 2014; Kang et al., 2009; Richoux et al., 2014). These results suggest different trophic niches of the different species. The authors suggested that the studied species partitioned resources in order to coexist. However, very little is known about how different co-existing taxa in the deep sea (corals, demosponges and bivalves) will be able to exploit varying food concentrations and types. Food availability varies widely on a temporal basis, with fluctuations occurring seasonally, daily and with the ebb and flood of the tide in their natural environment (Ludeman et al., 2017; Smith et al., 2013).

Equally, species interactions may lead to exploitative competition, meaning mediated by a reduction in resource availability without direct interaction between the competitors which raises the question: do co-existing species compete for food resources and can this competition be modulated by flow speeds?

On the Norwegian continental shelf VMEs are composed of the reef-building CWC *L. pertusa* commonly accompanied by demosponges (Fosså et al., 2002; Klitgaard and Tendal, 2004; Kutti et al., 2013; Mortensen, 2001), and by aggregations of the deep-sea bivalve *Acesta excavata* (Correa et al., 2005). Aggregations of these species offer an opportunity to answer the questions outlined above regarding food exploitation and competition between species.

Competition for food may be possible as *L. pertusa* has been documented to be an opportunistic feeder, taking up everything from zooplankton to Dissolved

Organic Matter (DOM) (Mueller et al., 2014; Naumann et al., 2011; Orejas et al., 2016). Sponges are documented to feed on picoplankton (<2 µm) (Reiswig 1975), and DOM. Finally, *A. excavata,* as other bivalves, are believed to preferentially feed on particles larger than 4 µm (Møhlenberg and Riisgård, 1978; Riisgård, 1988). Bivalves have also been documented to feed in smaller particles sizes, but not as efficiently (Charles et al., 1999, Silverman et al., 1995, Storhmeier et al., 2012), and some species such as *Geukensia demissa* were documented to feed on bacterioplankton both under laboratory and field conditions (Wright et al., 1982). To date the majority of feeding experiments on the aforementioned species have been done with artificial food sources, the present study used natural seston both characterised by particle sizes and type. This information will provide a better understanding of the feeding ecology of co-occurring species such as *L. pertusa, A. excavata, Geodia barretti, Phakellia Ventilabrum, Stryphnus* sp. and their interactions, and could be used to inform how ecosystem functioning of VMEs can change under changing conditions.

4.1.1. Aims

The aim of the present study is to better understand the feeding ecology, the nature of any competition interactions, and how these interactions might be affected by current speed changes and food availability in co-existing suspension feeders. The species used were the reef-forming coral *L. pertusa,* a passive suspension feeder; the sponges *G. barretti*, *Stryphnus* sp. and *P. ventilabrum* and the bivalve *A. excavata,* active suspension feeders*,* to test how they react to

different speed flows and concentration of natural seston and to assess preference for a specific particle size and type. More specifically to try an answer:

(i) Do active suspension feeders, sponges and bivalves, feed more efficiently under low flow conditions compared to passive suspension feeders such as *L. pertusa*?

(ii) Do *A. excavata, L. pertusa*, *G. barretti, P. ventilabrum and Stryphnus sp* feed preferentially on different particle sizes and types?

(iii) Do suspension feeders capture food more efficiently at higher food concentrations?

4.2. Materials and methods

4.2.1. Specimen collection and maintenance

Geodia barretti and *Stryphnus* sp. specimens were collected from Nakken reef (59°49'53 N, 5°33' 44 E DMS), and Langenuen Fjord (60°.00 37 N, 5°.19 14 E DMS), South-Western Norway (Figure 4.1), in April 2017. Samples were collected by the ROV *Aglantha* (FAMI AS, now Argus Remote Systems AS) on board the RV *Kristine Bonnevie*.

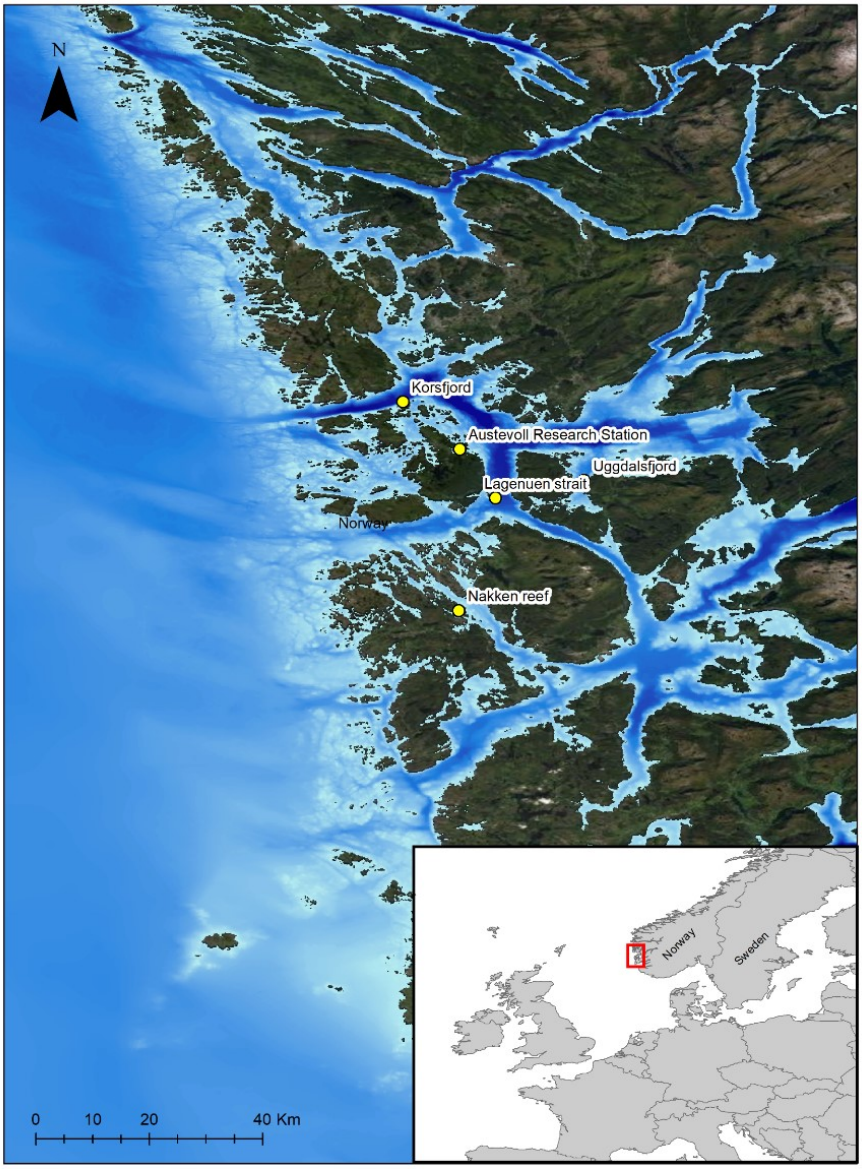


Figure 4.1: Map of collection sites in Norway

The collected sponges were cut into pieces of ca. 5*5*5 cm to produce explants (small pieces of living tissue cultivated to have more manageable pieces of the massive sponges). *Geodia barretti* and *Strypnus* sp. explants were cultivated in modified scallop cages at Uggdalsfjorden (60°02' 17N, 05°27' 43E DMS) (Figure 4.1) at 150 m depth. Fragments/explants of the aforementiones species do not survive in aquaria, hence the recovery has to be done *in situ* (Hoffmann et al., 2003)Explants were collected in November 2017 using the *Aglantha* ROV deployed from the RV *Hans Brattström* and were transported to the Norwegian Institute of Marine Research (IMR) Austevoll research facilities and placed in 1000 l tank with a flow of 2000 $l*h^{-1}$. The 7 months 'recovery time' in the field is considered to be sufficient for complete cortex (outer sponge tissue layer) regeneration, re-development of aquiferous systems, for normal pumping and respiration rates to resume, and for representative symbiotic microbial communities to re-establish (Hoffmann et al., 2003, 2006; Kutti et al., 2015).

The sponge *P. ventilabrum* was collected from Korsfjorden (60°9' 46.8N, 05°10.24E DMS) (Figure 4.1) with a trawling net on January 2018 on board of the RV *Hans Brattström*. Survival of *P. ventilabrum* after collection with trawling net was previously ascertained (Kutti, personal communication). The sponges were collected and kept on board using a flow-through aquarium system. Upon Arrival to IMR Bergen facilities, the sponges were placed in a flow-through 37 l tank before transportation to the Austevoll research facilities where they were put in the same tank with the other sponges. *Phakellia ventilabrum* individuals were cut to 5*5 cm fragments and left to acclimate for 2 months. After fragmentation*, P:*

ventilabrum does not need to recover in situ as do *G. barretti* and *Stryphnus* sp because they do not have a cortex (Martins et al., 2021). so they do not need regeneration time . Meaning that the fragments are fully functional.

Lophelia pertusa and *A. excavata* were collected from the Nakken reef (59°49'53 N, 5°33' 44 E DMS) (Figure 4.1) during the same cruise as *G. barretti* and *Stryphnu*s sp. Five coral colonies and the 30 *A. excavata* individuals were collected using the ROV. The organisms were taken from the seafloor from a depth ranging between 150 to 200 m using the automatic arm and placed into a collection basket attached to the ROV. Once on board, the specimens were placed in a 375 l tank until arrival to the IMR Austevoll research station. At the research station the corals were placed in a 1000 l tank with water flowing at 3000 l h^{-1}. The bivalves were placed in the same tank as described for *G. barretti* and *Stryphnus* sp. The specimens were maintained in the aforementioned lab conditions before the experiments started. Before starting experiments the *L. pertusa* colonies where fragmented into nubbins of approximately 10 polyps each, attached to marked putty epoxy bases and left to acclimate for 2 weeks. The water flowing through all the tanks was unfiltered seawater from 160 m deep, no extra food was added.

4.2.2. Experimental design

Each species was submitted to 6 different treatments designed with 3 flow speeds and 2 food concentrations (Table 4.1). Normal food concentrations were achieved with water from 160 m depth containing natural seston, high food concentrations were achieved by concentrating natural seston through a 41 µm

mesh over a 4 day period smaller meshes to target picoplankton were not available.

Table 4.1: Summary of experimental treatments

Flow speed / Food concentration	Low Speed 18.51 ± 0.63 l h^{-1}	Medium Speed 38.75 ± 1.45 l h^{-1}	High Speed 60.3 ± 1.82 l h^{-1}
Normal Food Natural seston, present in unfiltered deep-sea water (160m deep)	Low Speed Normal Food	Medium Speed Normal Food	High Speed Normal Food
High Food Extra seston was gathered for 4 days with a 41 µm mesh net, and added to unfiltered water supply	Low Speed High Food	Medium Speed High Food	High Speed High Food

Experiments were conducted in flow-through chambers as described in Strohmeier et al. (2009). These chambers were designed to achieve minimal recirculation helping prevent re-filtration. Chamber internal dimensions (w*l*h) were: 10.5 * 22 * 10 cm. Experiments were run in batches. Each batch consisted of 7 replicates of one treatment per species. Specimens were placed in the test chambers (Supplementary Material 4.1), and one chamber was left with a coral skeleton as a control for particle deposition (the control chamber was left empty when the sponges were being tested). The flow was set to the desired value and

measured before every experimental run for each chamber. The organisms were left to acclimate until filtering resumed (visible tentacles for *L. pertusa*, open oscula for the sponges, and open shell for *A. excavata*). For high food treatments, the concentrated seston was incorporated to the header tank with an electromagnetic metering pump EWN –R series IWAKI (JAPAN).

Water samples were simultaneously taken from the outflow of each chamber (7 with organisms and 1 control). Three subsamples of 10 ml were analysed with a PAMAS S4031 GO (Partikelmess-und Analysesysteme GmbH RUTESHEIM / GERMANY) particle counter analyser with 16 channels. Each channel counted particles of one predetermined diameter from 1 to 10 µm (nanoplankton). This range was chosen because previous preliminary tests showed that very few particles above that size range were in the water. When performing the High Food treatments the organisms were left to acclimate to the high food conditions for 2 h before taking the samples, this was done in order to avoid possible stress reaction to sudden particle increase. A 4^{th} subsample of each sample was taken, into 2 ml cryovials and fixed with 25% glutaraldehyde (final concentration 0.5 %) to preserve the picoplankton (bacterial and algal populations) and frozen at -80° until analysis by flow cytometry. Due to specimen numbers constraints, not all the species and treatments had the same amount of replicate runs and some of the specimens had to be re-used (Table 4.2 and 4.3).

Table 4.2: Number of experimental batches per species per treatment. Each batch had 7 replicates and one control chamber. *Lophelia pertusa* experiments were run between March and April 2018, *A. excavata* experiments were run in March April and end of May 2018, and *G. barretti*, *Stryphnus* sp. and *P. ventilabrum* experiments were performed between the end of May and the beginning of June 2018.

Species / Treatment	*L. pertusa*	*A. excavata*	*G. barretti*	*Stryphnus. sp*	*P. ventilabrum*
Low Speed Normal Food	3	4	2	2	1
Medium Speed Normal Food	2	4	2	2	1
High Speed Normal Food	0	4	2	2	1
Low Speed High Food	2	1	1	1	1
Medium Speed High Food	1	2	1	1	1
High Speed High Food	0	1	1	1	1

Table 4.3: Number of available specimens and their distribution across experimental treatments.

Species	Available specimens	Distribution on the different treatments runs.
L. pertusa	56	Different fragments for each run and treatment
A. excavata	28	Rotated randomly between the runs and treatments
G. barretti	14	The 7 specimens used in the first Normal Food treatments batch were re-used for the High Food batches
Stryphnus sp.	14	The 7 specimens used in the first Normal Food treatments batch were re-used for the High Food batch
P. ventilabrum	7	The 7 specimens were used for all treatments

In order to quantify the amount of POM and Suspended Particulate Matter (SPM) introduced to every batch, 10 l of water were collected from the control chamber (one replicate for every batch) and filtered through pre combusted, pre-weighed Gf\F filters (WHATMAN). Each filter was rinsed twice with 15 ml ammonium formate to eliminate salts as described by Strohmeier et al. (2009). Filters were subsequently dried for 24h at 60 °ºC, weighed and burnt for 4.5h at 450 °C and weighed again.

Following experiments, DW and organic carbon content of each organism from the different species was determined. *Lophelia pertusa* fragments were individually crushed with a pestle and mortar and placed into pre-weighed tin trays. *Acesta excavata* individuals were scooped out of their shells and put into pre-weighed trays. *Geodia. barretti* and *Stryphnus* sp individuals were sliced into

small pieces to speed up the drying process. *P. ventilabrum* individuals were placed into pre-weighed trays. All organisms were thereafter weighed in order to obtainwet weight, then left to dry at 60°C until dry weight was stable (2 weeks for *L. pertusa*, 2 days for the sponges, and 3 days for *A. excavata*). The trays were then burnt for 4.5h at 450 °C and weighed again, which gives the Ash Weight (AW). To obtain organic carbon content the AW was subtracted from the DW. The Ash Free Dry weigh (AFDW) was obtained, AFDW was used as a proxy for organic carbon content (Lucas, 1994). Organic content was then standardised to mol C g DW^{-1}.

4.2.3. Data analysis/ Clearance rate determination

The mean particle counts ml^{-1} obtained from the three subsamples analysed with the PAMAS were used to calculate size specific Retention Efficiency (RE), for each individual in every batch using the following equation:

$$RE=1-(PC_B/PC_C) \quad (1)$$

Where PC_C is particle count exiting the control chamber and PC_B is particle count exiting the experimental chamber. The RE *100 equates to the percentage of particles the organisms are retaining. The Clearance Rate (CR) was also calculated for each particle size, for each individual in every batch using the following equation:

$$CR=RE*F \quad (2)$$

Where RE is the previously calculated measurements and F is the flow in l h^{-1} measured for each chamber before each run.

The subsamples placed in the cryovials were analysed with BD LSR FORTESSA flow cytometer (BD Biosciences New Jersey USA) at the School of Biological Sciences, Institute of Immunology and Infection Research Flow Cytometry Core Facility, University of Edinburgh. The analyses were performed to account for bacterial and algal cells numbers. Samples were stained with SYBR green (Invitrogen, California USA), final concentration 0.02% in order to detect DNA. Algal and bacterial cells are differentiated because of chlorophyll and SYBR green dye fluorescence. The mean sizes of the particles were assessed from the forward scatter measurements provided by the flow cytometer. The number of SYBR green positive particles (particles containing DNA) were determined when plotting the counts in FSC (forward scatter) vs FITC (Fluorescein isothiocyanate) plots. DNA containing counts were plotted on a PerCP-Cy5-5 (Peridinin-chlorophyll proteins) vs FITC plot where gates were drawn in order to differentiate between green and red fluorescent particle (bacteria and algae respectively), see Figure 4.2. Gating is simply selecting an area on the scatter plot generated during the flow cytometry analysis. Polygons drawn on the scatter plots in order to select the cell population/ particles of interest. The process is subjective, but is based in prior knowledge of the particles being analysed (Figure 4.2).

All particles that did not contain DNA were considered silt. For each sample, the flow cytometer provided the total number of particles between 0.3 and 4 µm which was divided into total number of silt, bacterial and algal particles per 150 µl. Using these numbers, the RE and CR were calculated using equations

1 and 2 for bacteria, algae, and silt. Calculated CRs were normalised to mol C^{-1} (for both results coming from the PAMAS and the flow cytometer).

The results obtained for CR of particles of 1 µm were discarded. Particles of 1 µm are on the error zone of the PAMAS S4031 GO instrument. Negative CR were also excluded from the final analyses since the negative values meant that the analysed samples contained more particles than the control chambers which was likely due to particle production/release by the organisms (The percentage of positive results are summerised in suplemmentary materials 4.3 and 4.6).

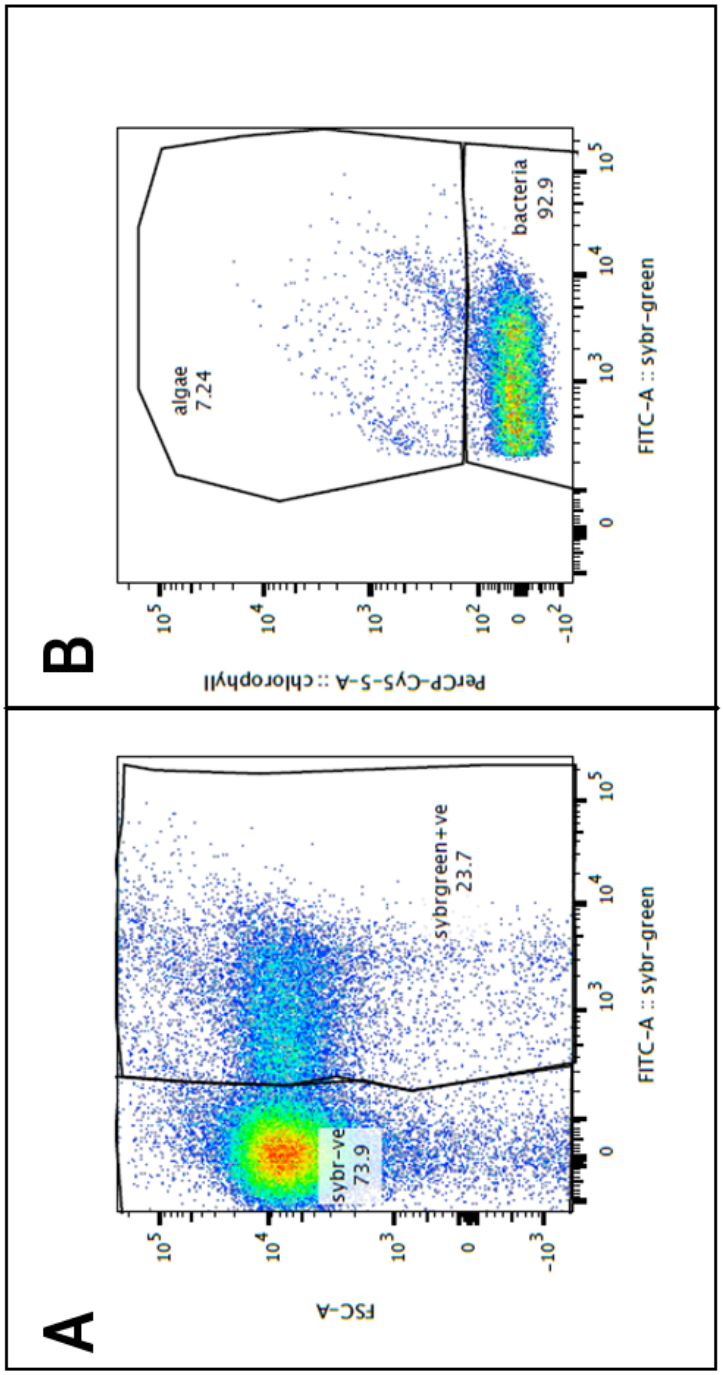


Figure 4.2: Cytogram showing the gating process. (A): All particle counts showed in the FSC vs FITC plot, the black line inside the plot represents the gate choosing SYBR-green positive particles. Numbers are the percentage of total counts allocated to each category. (B): PerCP-Cy5 vs FITC plot showing all particles recognised as SYBR green positive (containing DNA) the black line inside the plot represent the gates created to separate particle that exhibited Chlorophyll Fluorescence from just particles showing SYBR green fluorescence in order to differentiate between algae and bacteria. The numbers represent the percentage of SYBR green positive particles allocated to the different categories.

4.2.4. Statistical analyses

Data were analysed using R Studio 1.1.456 version statistical software (RStudio team, 2016). For each species and treatment, a linear model was used, were the dependent variable was the CR and the independent variable the particle size, measured as a categorical variable with n=9 levels: 2 to 10 µm, for each species. Due to the high skewedness of the CR distribution, a logarithmic transformation of this variable was applied to the data.

A linear model having particle size and treatment as independent variables was fitted for each species. In order to better asses the effect of the different treatments on the CR the concentration of particles from 3 to 7 µm was added and, the CR was then calculated. A linear model for each species was performed using CR as the dependent variable and treatment as an independent variable. To compare the averaged CR of the different species in each treatment a linear model was made where the CR was the dependent variable and the species the independent variable

The results coming from the flow cytometry were analysed using the same linear models as mentioned above, but the independent variable particle size was replaced by particle type.

To compare all the multiple factors for each species a post-hoc Tukey adjustments for pairwise comparisons with the lsmeans R package (Lenth, 2016) was used after each model.

4.3. Results

4.3.1. Pamas

Seston concentrations and subsequent carbon input varied between treatments (Supplementary Material 4.2). Particle concentration decreased with particle size for all treatments (Particle amount differences between Normal and High Food treatments for each species was statistically significant (p-value<0.0001).

For all species a different percentage of positive CR were found for each treatment, with a general trend of higher percentages found in Normal Food treatments (Supplementary Material 4.3). Average CR for each species under each treatment is summarised in Table 4.4. Negative CRs were interpreted as caused by particles released from the organisms or attributed to the high variability of the natural seston. For all species a trend was observed that indicated higher CR for bigger particle sizes where more than three positive results were found. Detailed results for each particle size CR for each treatment can be found in Supplementary Material 4.4, with significant results summarised in Supplementary Material 4.5. As a general trend sponges seem to prefer higher to medium flows. *Lophelia pertusa* seems to prefer low flow and *A. excavata* did not show a preference for any flow treatment (Table 4.4).

Table 4.4: Mean Clearance Rates (CR) for each species under each treatment. Dark grey values point to the highest CR for each species, while light grey highlighted values denotes lowest value for each species. Underlined values were calculated with less than 3 data points. NA: No available data.

Species	***A. excavata* CR** l h^{1} * mol C^{-1}	***L. pertusa* CR** l h^{-1} * mol C^{-1}	***G. barretti* CR** l h^{-1} * mol C^{-1}	***Stryphnus* sp. CR** l h^{-1} * mol C^{-1}	***P. ventilabrum* CR** l h^{-1} * mol C^{-1}
Low Speed Normal Food	118.62 ± 110.95	98.9 2 ±63.76	3.51 ± 2.06	2.79 ± 2.12	9.63 ± 4.49
Medium Speed Normal Food	110.78 ± 87.47	70.76 ± 55.48	3.58 ± 2.43	3.53 ± 3.16	23.10 ± 28.40
High Speed Normal Food	85.38 ± 64.16	NA	7.03 ± 6.87	6.60 ± 6.31	11.57 ± 5.57
Low Speed High Food	16.80 ± 23.69	65.31 ± 49.30	2.99 ± NA	NA	11.14 ±5.74
Medium Speed High Food	63.59 ± 68.54	51.94 ± 18.63	5.82 ± 2.54	3.95 ± 3.52	29.40 ± 2.19
High Speed High Food	117.16 ± 74.97	NA	NA	3.30 ± NA	24.36 ±30.64

4. 3.1.2. Comparison between species.

Generally the bivalve and coral *A. excavata* and *L. pertusa* presented on average 30 times higher CRs than the sponges *G. barretti* and *Stryphnus* sp. (Table 4.4). Statistical differences are accounted for below. Under Low Speed Normal Food, *A. excavata* showed the highest CR which was significantly higher than *G.*

barretti, Stryphnus sp. and *P. ventilabrum* (p-values: 0.0001, 0.0001, 0.0256 respectively). *Lophelia pertusa* also showed a significantly higher CR than *G. barretti, Stryphnus* sp. and *P. ventilabrum* (p-values: 0.0001, 0.0001, 0.0205 respectively) (Figure 4.3 A).

Under Medium Speed Normal Food, *A. excavata* had the highest CR and was significantly higher than the CR observed for *G. barretti* and *Stryphnus* sp. (p-values < 0.0001) (Figure 4.3 B). *Lophelia pertusa* had also a significantly higher CR than *G. barretti* and *Stryphnus* sp., (p-values 0.0008, and 0.0002 respectively) (Figure 4.3 B).

Under High Speed Normal Food, *A. excavata* had the highest CR and significantly higher CR than *G. barretti* and *Stryphnus* sp., (p-values <0.0001) (Figure 4.3 C). Under Low Speed High Food, the highest CR was observed for *L. pertusa*. No statistically significant differences were found between species (Figure 4.3 D). Under Medium Speed High Food, *A. excavata* had the highest CR. *Stryphnus* sp. had a significantly lower CR than *A. excavata* and *L. pertusa* (p-values 0.0153 and 0.0175 respectively) (Figure 4.3 E). Finally, under treatment High Speed High Food, *A. excavata* had the highest CR which was significantly higher than the CR for *Stryphnus* sp. (p-value 0.0001) (Figure 4.3 F).

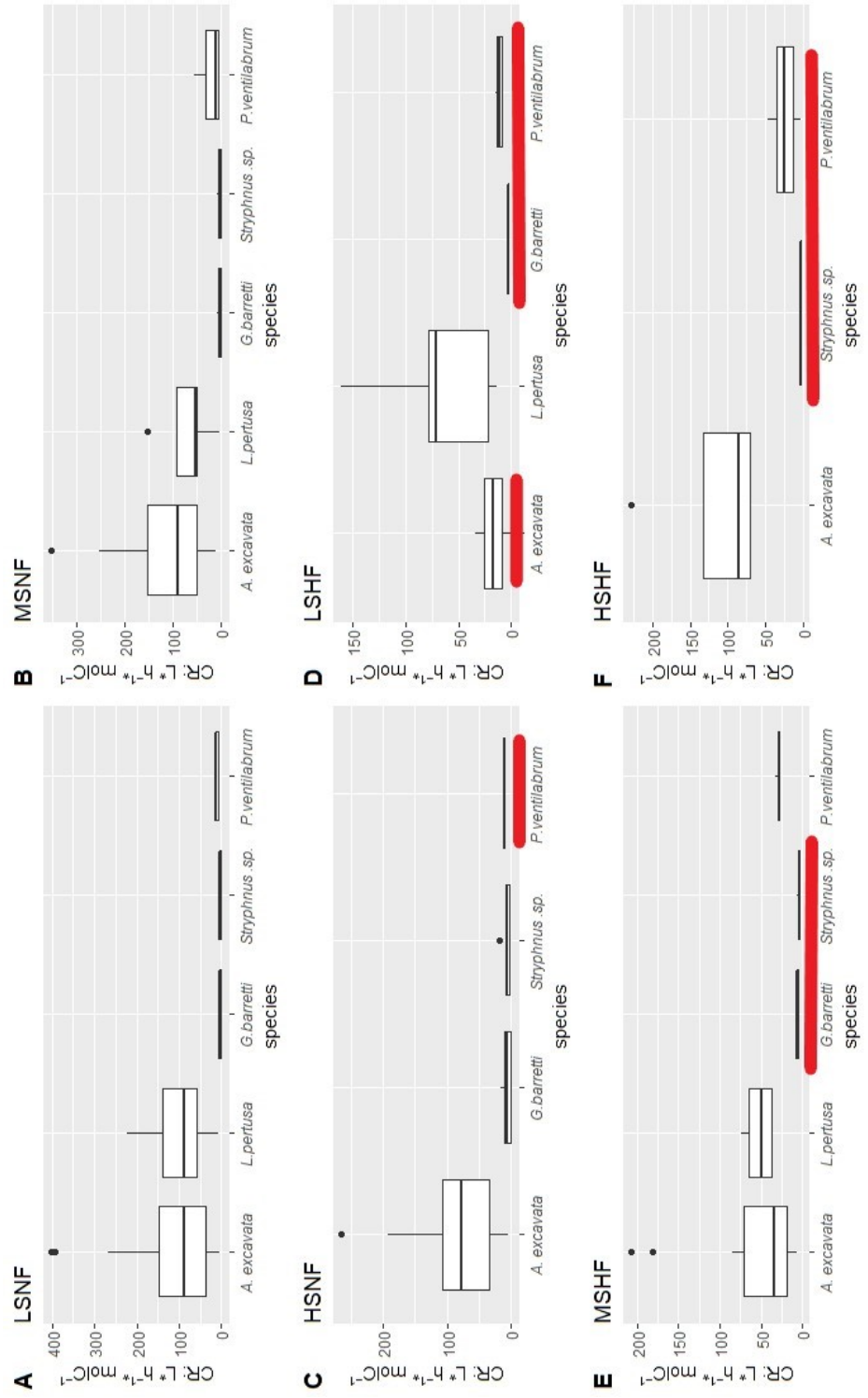


Figure 4.3. Boxplots showing the CR calculated for each species under the different treatments. The red lines under the boxplots signal that the marked treatments have less than 3 data points, hence results should be taken with caution. (A): Low Speed Normal Food. (B): Medium Speed Normal Food. (C): High Speed Normal Food. (D): Low Speed High Food. (E): Medium Speed High Food. (F): High Speed High Food. Black dots represent outliers.

4.3.2. Flow cytometry results

For flow cytometry, algae had a mean size of 4.39 ± 0.8 µm, bacteria had a mean size of 0.52 ± 0.2 µm. The particles categorised as silt ranged from 8 to 0.3 µm and comprised all the particles that did not have DNA or had chlorophyll fluorescence. Percentage of positive results for all Normal and High Food treatments and all particle types can be seen in (Supplementary Material 4.6)

4. 3.2.1. Acesta excavata

For all particle types the highest CR was achieved under High Speed Normal Food conditions and reached 216.62 ± 194.04, 124.96 ± 76.49 and 186.10 ± 185.59 l h-1 * mol C^{-1} silt, algae and bacteria respectively. Under Medium Speed High Food, the average CR for algae was 141.20 ± 224.48 l h^{-1} * mol C^{-1} (Table 4.5). This result is not presented as the highest outlier elevated the mean. A trend is evident that *A. excavata* is more efficient at higher flows under Low food conditions. No such trend was observed under High food conditions. No interactions between CR and particle type were found.

4.3.2.2. Lophelia pertusa

For all three particle types: silt, algae and bacteria, *L. pertusa* had the higher CRs under Medium Speed Normal Food and reached: 110.71 ± 67.88, 72.28 ± 55.60, 259.24 ± 198.37 l h^{-1} * mol C^{-1} respectively. Under Medium Speed Normal Food the CR for bacteria is significantly higher than for algae (p-value 0.00329). The CR for bacteria in Medium Speed Normal Food is statistically significantly higher than in Low Speed Normal Food (p-value 0.0019), (Table 4.5). Trends suggest that bacteria are the particles consumed more efficiently under Medium

flow Normal food conditions compared to Low Speed Normal food. No such trend was observed under the High Food treatments

4.3.2.3. Geodia barretti

Geodia barrettti exhibited the highest CRs for bacteria and algae in Medium Speed Normal Food and reached; 54.32 ± 34.42, 50.46 ± 38.63 l h^{-1} * mol C^{-1} respectively. For silt particles the highest CR was under High Speed Normal food and reached 21.04 ± 22.19 l h^{-1} * mol C^{-1}. Overall, *G. barretti* showed lower CRs for silt particles under all treatments compared to the other four species, significant results can be summarised as follows: at Low Speed Normal Food, algae/silt (p-value =0.04). Under Medium Speed Normal Food Bacteria/silt (p-value 0.01). Under treatment High Speed Normal food algae/silt (p-value 0.03). Under Low Speed High Food bacteria/silt (p-value 0.04). Under Medium Speed Normal Food, silt presented a significantly lower CR than bacteria (p-value 0.03). The CR for bacteria and algae were significantly higher under Medium Speed Normal Food compared to Low Speed Normal Food (p-value 0.00025, 0.043), and it was also significantly higher in Medium Speed High Food than Low Speed Normal Food (p-value 0.022) (Table 4.5).

4.3.2.4. Stryphnus sp.

Stryphnus sp. had the highest CR under High Speed Normal Food for silt, algae, bacteria and attained 15.42 ± 10.14, 29.88 ± 15.44, 40.39 ± 20.84 l h^{-1} * mol C^{-1} respectivelly. For bacteria, the CR in High Speed Normal Food was significantly higher than in Low Speed High Food and Medium Speed Normal Food (p-values 0.00001 and 0.009). For the same particle type, the CR was significantly higher in

High Speed High Food than Low Speed High Food (p-value 0.048). Trends for algae and silt on the Normal food treatment also suggest that *Stryphnus* sp. is more efficient at High Flow speeds. No such trends were found under High Food treatments.

In treatment Low Speed High Food CR for algae was significantly higher than for bacteria, (p-value 0.0049). Overall trends show higher CRs under all treatments for algae and bacteria, except under Low Speed Normal Food (Table 4.5).

4.3.2.5. Phakellia ventilabrum

For silt, algae, bacteria; CR was highest in Medium Speed Normal Food treatment and reached 377.79 ± 171.78, 258.82 ± 116.11, 252.39 ± 100.15 l h^{-1} * mol C^{-1} respectively.

Under Medium Speed High Food, the CR for algae was significantly lower than for silt and bacteria (p-values 0.014 and 0.0004). The CR for algae was significantly lower under Medium Speed High Food than under Medium Speed Normal Food, High Speed Normal Food, and High Speed High Food, (p-values: < 0.0001, 0.04, 0.01). Under Medium Speed Normal Food, CR for algae was significatly higher than under Low Speed Normal Food (p-value 0.0001). For silt the CR was statistically higher under Medium Speed Normal Food than in Medium Speed High Food (p-value 0.02). *Phakellia ventilabrum* presented a significantly higher CR for bacterial particles under Medium Speed Normal Food compared to Low Speed Normal Food (p-value 0.012) (Table 4.5). Generally in all treatments CRs were higher for silt and bacteria for all treatments with the exception of High Speed High Food.

4.3.2.6. Comparison amomg species

Generally *A. excavata* had higher CRs than *G. barretti* and *Stryphnus* sp. Under Low Speed Normal Food, *A. excavata* exhibited the highest CRs for all particle types, and presented a significantly higher CR for silt particles than *G. barretti* (p-value 0.001). *Acesta excavata* had also a higher CR for algae than *Stryphnus* sp., (p-value 0.02) (Table 4.5, Figure 4.4 A). Under Medium Speed Normal Food, *P. ventilabrum* showed the highest CRs for silt and algae, and *L. pertusa* exhibited the highest average CR for bacteria. For silt particles, *A. excavata* showed significantly higher CR when compared with *G. barretti* and *Stryphnus* sp. (p-values 0.035, 0.043), and *P. ventilabrum* showed a significantly higher CR than *G. barretti* and *Stryphnus* sp (p-values <0.0001). For algal particles *P. ventilabrum* presented a significantly higher CRs when compared to *Stryphnus* sp. and *G. barretti* (p-values 0.0001, 0.02), and *A. excavata* had a significantly higher CR for algae than *Stryphnu*s sp. (p-value 0.01). Finally, for bacterial particles *Stryphnus* sp. exhibited significantly lower CRs than all the other species (p-values 0.0001, 0.004, 0.001, 0.03). Finally *L. pertusa* presented a significantly higher CR for bacteria when compared to *A. excavata* (p-value 0.03) (Table 4.5, Figure 4.4 B).

Under High Speed Normal Food *A. excavata* had the highest CRs for all particle types. For silt particles *A. excavata* had a significantly higher CR than *G. barretti* and *Stryphnus* sp. (p-value < 0.0001). For algal particles *A. excavata* had a higher CR than *Stryphnu*s sp. (p-value 0.0006). For bacterial particles*, A. excavata* had a significantly higher CR than *G.barretti* and *Stryphnus* sp. (p-values 0.0001, 0.0007),

and *P. ventilabrum* exhibited a higher CR than *G. Barretti*. (p-value 0.0002) (Table 4.5, Figure 4.4 C).

Under Low Speed High Food, *A. excavata* had the highest CRs for algae and bacteria and *P. ventilabrum* showed the highest CR for silt. (Table 4.5). For silt particles *P. ventilabrum* showed a significantly higher CR than *G. barretti* and *Stryphnus* sp. (p-values 0.0001, 0.007), and *L. pertusa* had a significantly higher CR than *G. barretti* (p-value 0.01). Note that *G. barretti* under Low Speed High Food for silt particles consisted just of two data points. For algal particles, *G.barretti* showed a significantly lower CR than *L. pertusa, P. ventilabrum* and *A. excavata*, (p-values 0.002, 0.006, 0.01). For bacterial particles *Stryphnus sp.* exhibited a significantly lower CRs than *P. ventilabrum*, *L. pertusa* and *A. excavata* (p-values 0.0001, 0.0007, 0.006) (Table 4.5, Figure 4.4 D). Under Medium Speed High Food *A. excavata* exhibited the highest CRs for silt and algal particles, while *P. ventilabrum* had the highest CR for bacteria. No statistical differences were found in between the species (Table 4.5, Figure 4.4 E). Under High Speed High Food treatment *P. ventilabrum* showed the highest CR for all particle types. No statistical differences were found in between the species (Table 4.5, Figure 4.4 F).

Table 4.5 *Average of the estimated CRs for all species under the different treatments and for the different particle types. Dark grey values point to the highest CR for each species, while light grey highlighted values denotes lowest value for each species. Underlined values were calculated with less than 3 data points. NA: No available data.*

Treatment	Particle type	***A. excavata*** **CR** l h^{-1} * mol C^{-1}	***L. pertusa*** **CR** l h^{-1} * mol C^{-1}	***G. barretti*** **CR** l h^{-1} * mol C^{-1}	***Stryphnus* sp.** **CR** l h^{-1} * mol C^{-1}	***P. ventilabrum*** **CR** l h^{-1} * mol C^{-1}
Low Speed Normal Food	Silt	110.81 ± 121.27	27.78 ± 34.29	3.30 ± 2.34	12.40 ± 8.77	37.44 ± 28.74
	Algae	57.76 ± 71.55	32.62 ± 37.39	11.58 ± 7.24	4.56 ± 3.08	16.09 ± 12.18
	Bacteria	66.47 ± 66.44	14.25 ± 12.00	7.19 ± 4.92	12.02 ± 6.91	37.91 ± 28.04
Medium Speed Normal Food	Silt	106.90 ± 62.50	110.71 ± 67.88	16.19 ± 11.49	12.65 ± 4.43	377.79 ± 171.78
	Algae	97.25 ± 76.35	72.28 ± 55.60	50.46 ± 38.63	17.17 ± 12.98	258.82 ± 116.11
	Bacteria	73.50 ± 70.63	259.24 ± 198.37	54.32 ± 34.42	14.18 ± 10.92	252.39 ± 100.15
High Speed Normal Food	Silt	216.62 ± 194.04	NA±NA	21.04 ± 22.19	15.42 ± 10.14	69.43 ± 221.37
	Algae	124.96 ± 76.49	NA±NA	47.07 ± 22.91	29.88 ± 15.44	78.82 ± 49.26
	Bacteria	186.10 ± 185.59	NA±NA	24.58 ± 13.51	40.39 ± 20.84	182.23 ± 204.44
Low Speed High Food	Silt	13.61 ± NA	44.94 ± 52.67	0.79 ± 0.59	4.56 ± 4.65	115.14 ± 118.96
	Algae	84.32 ± 73.55	68.55 ± 61.97	3.83 ± 3.59	12.62 ± 7.72	70.86 ± 83.74
	Bacteria	87.45 ± 110.71	55.33 ± 56.88	15.42 ± 2.94	2.92 ± 2.69	73.12 ± 61.52
Medium Speed High Food	Silt	93.29 ± 123.85	91.38 ± NA	2.32 ± NA	7.78 ± 1.71	46.55 ± 32.31
	Algae	141.20 ± 224.48	31.20 ± NA	NA±NA	11.36 ± 8.15	18.65 ± 26.58
	Bacteria	42.33 ± 32.29	31.00 ± 43.34	37.69 ± 8.67	6.16 ± 4.55	63.70 ± 33.00
High Speed High Food	Silt	59.90 ± 66.24	NA±NA	22.86 ± 15.98	3.13 ± NA	109.81 ± 142.95
	Algae	49.07 ± 49.39	NA±NA	NA±NA	7.52 ± 4.00	69.20 ± 40.03
	Bacteria	23.22 ± 34.73	NA±NA	21.74 ± 11.40	16.00 ± 5.88	73.31 ± 36.76

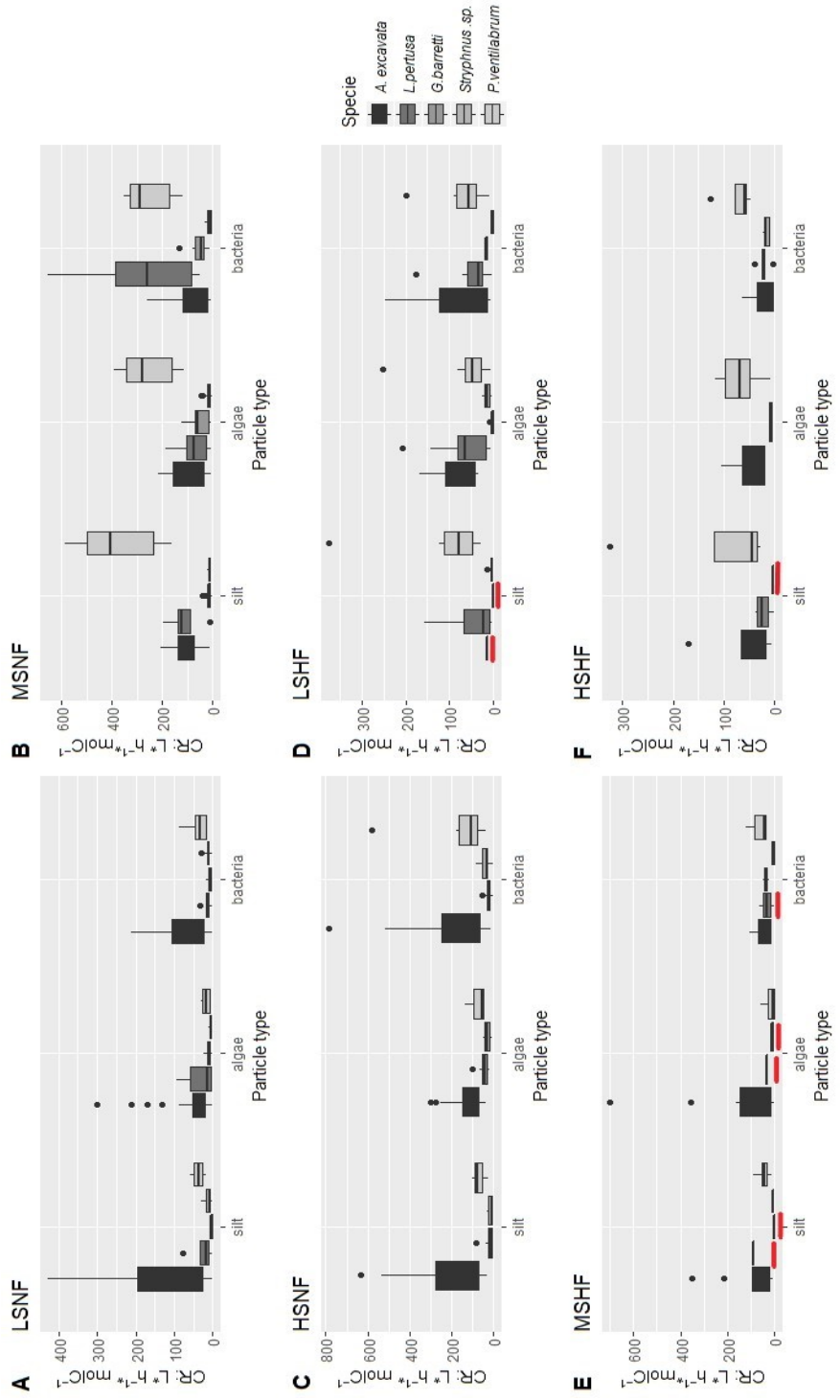


Figure 4.4 Boxplots showing the CR calculated for each species for each particle type under the different treatments. The red lines under the boxplots signal that the marked treatments have less than 3 data points, hence those results should be taken with caution. (A): Low Speed Normal Food. (B): Medium Speed Normal Food. (C): High Speed Normal Food. (D): Low Speed High Food, (E): Medium Speed High Food. (F): High Speed High Food. Black dots represent outliers.

4.4. Discussion

Generally the bivalve *A. excavata,* and the coral *L. pertusa* presented on average 30 times higher CRs than the sponges *G. barretti* and *Stryphnus* sp. with statistical differences determined through PAMAS results. The flow cytometry results also revealed higher CRs for *L. pertusa, A. excavata* and *P. ventilabrum* for all particles when compared to *G. barretti* and *Stryphnus* sp.

In accordance with the high CR found for *A. excavata* in this study, Järnegren and Altin (2006) found high CR of 13.36 l h^{-1} g^{-1} DW for this species, however the CR reported in Järnegren and Altin (2006) is higher than the one presented on this study, most likely, due to differences in methodologies. The present study measured CR in an open system using natural occurring seston, while Järnegren and Altin (2006) used recirculating systems and lab reared microalgae as a food source. Comparing the obtained CR results for *L. pertusa* in this study to relevant coral feeding literature is not straightforward since previous studies quantify its efficiency as capture rate per polyp, and have used artificial food and used recirculation systems.

The CR for *G. barretti* was low, which is in agreement with the specific filtration rate of 0.02 l h^{-1} ml $^{-1}$ tissue, calculated by Leys et al. (2018) and this filtration rate is considered to be low compared to other sponges (Leys et al., 2018). Though direct comparison is difficult due to different methodology. The filtration rate calculated by Leys et al (2018) is defined as the excurrent velocity multiplied by the area of the osculum. This measures the amount of water the sponge is able to process, not the percentage of particles cleared from the

processed water as does the CR. In general, when comparing CRs or filtration rates amongst sponges, differences are found between High Microbial Abundance (HMA) and Low Microbial abundance (LMA) sponges, this distinction indicates differing traits between the sponges (De-Goeij et al., 2017). *Geodia barretti* and *Stryphnus* sp. are HMA sponges and are defined as containing 10^8 to 10^{10} bacteria g^{-1} sponge tissue (Hentschel et al., 2006; Reiswig, 1981; Webster et al., 2001). *Phakellia ventilabrum* is a LMA sponge (Morganti et al., 2017) and is defined as having microbial abundances similar to those found in seawater 10^5 to 10^6 bacteria g^{-1} sponge tissue (Hentschel et al., 2006). Differences between HMA and LMA sponges were also observed in this study as discussed in section 4.4.2. The results from the sponges would have been more representative with more independent replicates and higher replication numbers.

4.4.1. Effects of flow

The question "Do active suspension feeders, sponges and bivalves, feed more efficiently under low flow conditions compared to passive suspension feeders such as *L. pertusa*?" Trends suggest that sponges are more effective under High and Medium speeds and so is *A. excavata*. *Lophelia pertusa* is slightly more effective under lower flows. The trends found are opposed to the evidence that seston flux is an important factor affecting the organismal performance of passive suspension feeders, whereas the seston concentration is more relevant for active ones as suggested by Lesser et al. (1994) and Gili and Coma (1998).

The present study suggests that *L. pertusa* is an effective suspension feeder under the different food and flow conditions tested, in accordance with its

previously documented opportunistic behaviour (Maier et al., 2019; Mueller et al., 2014; van Oevelen et al., 2016). It is worth noting that the flow speeds tested were low compared to other studies (Orejas et al., 2016; Purser et al., 2010), but the same trend as in the aforementioned studies is apparent, *L. pertusa* is more efficient at capturing prey at lower flow conditions. The amount of positive results for *L. pertusa* in Low Speed Normal Food treatments was lower for the results calculated from flow cytometry data than for PAMAS. This can possibly be explained because of sample degradation, the particles might have desitegrated into smaller ones. Hence, the results for Low Speed Normal Food treatment for *L. pertusa* are deemed to have low confidence.

To the author's knowledge, all known *L. pertusa* feeding studies have been done with relatively small nubbins, and not entire colonies. Entire colonies c modulate flow regimes (Mienis el at., 2019), hence the regimes experienced by the different polyps or parts of the colony can be different than the overall above colony speed. The relationship between flow speed and feeding efficiency can also be modulated by overall colony morphology and polyp density as discussed for *D. meteor* and *V. flagellum* in Chapter 3. In the middle of the colonies, polyps are likely to experience reduced flows (Purser et al., 2010; Sebens and Johnson, 1991), ergo they would benefit from overall higher flow speeds because the water flow will be reduced by the colony structure. While polyps in the periphery of the colony would benefit of overall lower speeds, this has been documented for tropical corals (Wijgerde et al., 2012). The differences in flow represent distinct optimum feeding speeds that can be utilised to catch different prey items (De

Clippele et al., 2018). *Lophelia pertusa* in the present study filtered more bacteria in Medium Speed Normal Food treatment, which is in accordance with previous studies. Results by Orejas et al. (2016) showed that at higher speeds, *L. pertusa* has a higher efficiency capturing small particles, conversely at lower flows *L. pertusa* captured bigger particles more efficiently. The tested current speeds in this study were overall lower than the lowest used by Orejas et al. (2016), hence parallels between the results are difficult to do.

Phakellia ventilabrum showed the highest CR for all particle types under Medium Speed Normal Food treatment, which suggest that given specific conditions *P. ventilabrum* can be more efficient than the other tested species. This trend was not evident in the analysis issued from the PAMAS, but both results confirm *P. ventilabrum* preference for medium flow speed.

Trends suggesting that active filter feeders are more effective under Medium and High flows is in accordance with the hypothesis that active suspension feeders are able to use ambient flows to reduce the cost of pumping (Leys et al., 2011; Vogel, 1970) or they benefit from the increased availiability of particles per unit of time, without limitation or collapse of their filtration structures.

4.4.2. Preferences for different food items

The PAMAS results revealed increasing CR with increasing particle size for all the species. All particle sizes tested are on the recorded spectrum for all the species considered (Järnegren and Altin, 2006; Mueller et al., 2014; Witte et al., 1996). The results for *A. excavata* and *L. pertusa* suggest that they are

opportunistic feeders (Maier et al., 2019; Mueller et al., 2014; van Oevelen et al., 2016). The fact that *A. excavata* feeds on bacteria suggest that this species is more versatile than previously thought, as confirmed by Maier et al. (2020) documenting *A. excavata* feeding on bacteria and DOM.

Deep-sea bivalves are known to be adapted to low food availabilities, by having a high filtration efficiency (Oliver, 1979), as recorded in this study and by Järnegren and Altin (2006). However, it is not known if *A. excavata* is as opportunistic as *L. pertusa*, hence if food resources are affected, reducing quality, quantity or diversity because of global change as predicted (Campanyà-Llovet et al., 2017; Levin and Le Bris, 2015; Sweetman et al., 2017), *L. pertusa* could possibly outcompete *A. excavata.* It is also worth noting that very little information is available on the feeding ecology of *A. excavata.* Nevertheless, the ability for bivalves to change their diet and filtration efficiency due to seasonal changes has already been documented (Cranford et al., 1999; Stroheimer et al., 2012).

Overall *P. ventilabrum* had a higher CR than *G. barretti* and *Stryphnus* sp. The fact that *P. ventilabrum* showed a trend suggesting a preference for silt and bacterial particles above algae hints that this species relies more on bacteria and silt than *Stryphnus* and *G. barretti*. Results suggest that *Stryphnus* and *G. barretti* have a preference for algal and bacterial particles (exception being *G. barretti* under Medium Speed High Food and High Speed High Food treatment were no positive results for algae were found) further suggesting a more selective feeding strategy in sponges. *Geodia barretti* and *Stryphnu*s sp are HMA sponges, and *P.*

ventilabrum is an LMA sponge (Schhöttner et al., 2013). The HMA and LMA sponges are structurally different, the former having a more dense tissue and an aquiferous system designed to increase contact time between seawater and sponge (Weisz et al., 2008). On the contrary, LMA sponges have a more porous tissue (Weisz et al., 2008). This difference can explain the higher CR for *P. ventilabrum*. High microbial abundance sponges are recorded to have lower pumping rates compared to LMA sponges (Maldonado et al., 2012; Weisz et al 2008). Furthermore, HMA sponges have also been hypothesised to complement their diet with their own symbionts and a more important role of DOM in their nutrition (De Goeij et al., 2017; Leys et al., 2018; Yahel et al., 2003). The fact that HMA and LMA sponges studied showed preference for different particle suggests that they do not directly compete. Tropical sponges have been found to have low functional redundancy and to differentiate between types of bacteria as a food source (Perea-Blázquez et al., 2013). Other studies have also pointed out that sponges can discriminate between particles of similar sizes (Leys and Eerkes-Medrano, 2006; Maldonado et al., 2010; Yahel et al., 2006, 2007) hence the sponges are not necessarily in direct competition. Characterising and quantifying the DOM can also give valuable information since sponges are known to feed on it (Maldonado et al., 2012; De Goeij et al., 2017) and laboratory records suggest that *L. pertusa,* other cold water scleractinians and *A: excavata* can also incorporate carbon from DOM (Gori et al., 2014; Maier et al., 2020; Mueller et al., 2014).

Part of the DOM consumed by sponges can be converted to detrital Particulate Organic Matter (POM) a process that has been characterised and named the sponge loop (De Goeij et al., 2008; 2009; 2013; Rix et al., 2016). The transformation of DOM into POM can explain how the different studied species are able to co-exist. The POM detritus produced by sponges using DOM from coral mucus has already been observed to be utilised by other detritivores in tropical reefs (Nauman et al., 2010; Rix et al., 2018). Following this argument, it has also been documented that mucus released by *L. pertusa* and *M. oculata* is also used as food for marine microbes (Wild et al., 2008), which in turn will be consumed by sponges, further minimising possible competition. Additional investigation of the sponge loop in CWC reefs might elucidate even further C and N processing in the deep sea, and might explain the niche overlap found between *L. pertusa* and *Hymedesmia coriacea* found by van Oevelen et al. (2018). Equally pseudo faeces of *A. excavata* have been showed to represent a food source for deposit feeders such as ophiuroids (Maier et al., 2020), hence it could be possible that resuspended pseudofecal material is a food source for sponges and corals. Pseudofeces could be caught in mucus filaments of *L. pertusa* and be consumed by it or made more available to sponges which consume the mucus.

It has been shown that *L. pertusa* in its natural habitat feeds predominantly on calanoid copepods (Dodds et al., 2009; Osterloff et al., 2019) and bivalves have also been documented to feed on zooplankton (Green et al., 2003; Lehane and Davenport, 2002; Pace et al., 2002; Pehadra et al., 2012). The three sponges species tested are not carnivorous (Hestetun et al., 2016) and are limited to

consuming particles < 50µm because of ostia size (Maldonado et al., 2012). Hence it can be suggested that in periods where zooplankton is available, more of the smaller seston will be available for sponges, minimising possible competition.

Without a more detailed characterisation of seston particles and their quantiy, it is very difficult to affirm if they compete and if their competition is exploitative meaning mediated by a reduction in resource availability without direct interaction between the competitors. Especially considering that in order for exclusive competition to take place food needs to be a limiting factor (Gause 1934).

4.4.3. Effects of food concentration

For all the tested species, High Food treatments had an overall lower CR than for all the Normal Food treatments, which suggest that they can get stressed or are sensitive to high particle concentration. Especially for *A. excavata*, this phenomenon has been already reported for bivalves (Cahalan et al., 1989; Jørgensen, 1990). The trends observed for *A. excavata* suggest indeed that this species is affected by high particle concentration, but this reaction seems to be less severe at higher flows, which might be explained by the fact that higher water flows could clear the feeding apparatus from clogging. This argument can be further reinforced by the fact that consistently, for all the species, a lower percentage of positive results were found in High Food treatments (Table 4.5). Negative results suggests that the organisms were releasing particles, potentially pseudo-faeces in the case of *A. excavata* (Deslou-Paoli et al., 1992). In the case of sponges, particle release can be explained by cell shedding, as sponges have been

found to have a high cell turnover (Alexander et al., 2014; De Goeij et al., 2009). The results suggest that none of the tested species were able to take advantage of the higher food concentration. Campanyà-Llovet et al. (2017) suggested that food quality is more important for biodiversity in the deep sea compared to quantity. It is worth noting that the gathered seston could have had a higher percentage of non-organic material. Excess inorganic material can clog the filtering system of sponges and can cause reduction in pumping rates (Bell et al., 2015; Kutti et al., 2015; Tomkins-MacDonald and Leys, 2008). Higher natural occurring detrital organic matter has been documented to reduce, although not significantly, the pumping rates of 5 different species of sponges (Morganti et al., 2019). Bivalves are also affected by excess suspended sedimentation, by producing more pseudo faeces (Ward and Shumway, 2004), and can reduce gap opening and filtration rates (Jørgensen, 1990). Ellis et al., (2002) also documented populations of the bivalve *Atrina zelandica* living in high sedimentation regimes to have a lower physical condition when compared to populations experiencing lower sedimentation regimes. Finally, other CWCs, *Primnoa resedaeformis* and *Duva florida* have been documented to modify their food intake when exposed to high inorganic sedimentation (Liefmann et al., 2018). Conversely, *L. pertusa* behaviour did not significantly change when exposed to drill cuttings (Mortensen et al., 2015), but live tissue cover of the skeleton (coenosarc) has been documented to decrease (Larsson et al., 2013b; Baussant et al., 2018).

4.5. Conclusions

- Taxa differences in feeding efficiency were observed, sponges had lower CRs than the two other taxa. This trend was observed for both results obtained from the PAMAS and flow cytometry with the exception being *P. ventilabrum* under Medium Speed Normal Food treatment. Though the CRs from all the three sponges are higher for the flow cytometry results because the latter technique focuses on particle type instead of size, which suggest that sponges are selective suspension feeders. The trends found this study represent relevant information of CR for prey items found in natural environments in flow through systems, which represent a more realistic situation.
- The tested current speeds did not affect CRs significantly but the observed trends evidenced that the different species could exploit different flows depending on the food items available and their feeding strategy and possibly due to the different traits the species present. More in depth experiments encompassing a broader range of flow speeds, could shed some light on how the predicted flow changes because of global change will affect the feeding efficiencies. Equally better results could be achieved having a higher replicate number and independent replicates. Another aspect to take into account is the fact that not much information is known on how big and how long lasting changes could be; if changes are periodical, the different species could possibly exploit the differences.

- On the other hand, high food treatments tested in this study seemed to have a negative effect on the species tested, suggesting higher food availability does not increase feeding efficiency, also suggesting sensitivity to excess particles in the water column. It is worth noting that increased sedimentation because of incremented precipitation on land and glacier retrieval (Ramirez-Llodra et al., 2011; Sweetman et al., 2017) can aggravate the aforementioned sensitivity.

  In the case of food scarcity, other qualities such as lipid storage can play a role in the survival of either one species, which can be key in determining survival. *Lophelia pertusa* has been documented to withstand fasting periods (Maier et al., 2019), but not such research has been undertaken for the other 4 species.

- Further characterisation of the available seston and its temporal and spatial variability should be undertaken, in order to better understand possible competition and how species might take advantage of the different seston items and temporal niches created by seasonal and daily variations in hydrodynamic conditions and prey diversity. Also, Mortensen et al., (1995) concluded that bottom current and turbulence affect faunal distribution in *L. pertusa* bioherms, so competition should also be studied in relation to the spatial positioning of the co-existing species. Finally other stressors that would be brought by global change would affect species metabolism and their interactions, for example higher temperatures could reduce the

amount of mucus produced by corals (Levas et al., 2015), which could reduce the importance of the sponge loop in mediating species co-existence by enabling nutrient recycling. Abiotic changes such as temperature increase, and ocean acidification should form an important component of future competition studies.

Chapter 5: Synoptic and Integrated Discussion vulnerable marine ecosystem indicator taxa in a changing ocean

Vulnerable marine ecosystem indicator taxa are diverse, taxonomically and functionally, but little is known about the interactions of the co-occurring species. The aim of this thesis was to relate the differences between species to their possible interactions, more specifically competition and performance (e.g. feeding efficiency), and quantify how these interactions can be modulated by different abiotic conditions such as flow or food availability, which has been projected to change in response to climate change (Caesar et al., 2018; Collins et al., 2019; Frajka-Williams et al., 2019; Holt et al., 2018; Thornalley et al., 2018; Schmittner et al., 2008; Sweetman et al., 2017).

Cold-water corals have several quantifiable traits that are of particular relevance to this. These include skeletal composition, sclerite shape and size, and morphology. Differences in these traits and species attributes may help elucidate species interactions, such as possible competition, and can also enable stable co-existence (Kraft et al., 2015b; Webb et al.,2002), or how they could adapt under changing conditions.

Chapter 2: this chapter explored two traits of co-occurring species from the Condor seamount: *V. flagellum* and *D. meteor*. Skeletal composition, sclerite shape and size, and the differences in elemental composition were assessed. The potentially stiffer skeleton of *V. flagellum* was found to have a higher calcitic content, whilst the potentially more flexible skeleton of *D. meteor* was found to be mostly organic.

Lewis and Esford (1987) suggested that octocorals having a stiffer skeleton are adapted to calm hydrodynamic environments, while octocorals having a more flexible skeleton could be adapted to surge type hydrodynamics. *Viminella flagellum* is found in a low to moderate flow environment (Giusti et al., 2012; Tempera et al., 2012), which is potentially facilitated by the stiffer properties of its skeleton. *Dentomuricea meteor* occurs in high flow regimes (Braga-Henriques et al., 2013; Tempera et al., 2012), which could also be facilitated by a more flexible skeleton. The double head sclerites found in *V. flagellum* could enhance its stiffness. The spindles found in *D. meteor* could enable rotational capacity (Lewis and Wallis, 1991), which could in turn be important when living under high flow systems. When found co-occurring, the different traits present in the species (skeleton composition and sclerite shape and size) investigated in this chapter are thus likely to represent different strategies by the two octocorals which can enable the two species to exploit the different conditions encountered in the Condor seamount. The different hydrodynamic conditions are further explained in Bashmachnikov et al. (2013). The different strategies minimise possible competition by creating stabilising effects as defined by Chesson (2000). The traits and strategies could be tailored to the life history and feeding preferences of the different species. To understand the interactions between coexisting species in more detail, more traits and multiple ecological dimensions should be taken into consideration. Especially because stabilising effects result from species differences in multiple ecological dimension (Kraft et al., 2015b)**,** meaning different traits that act in different contexts (i.e. feeding, reproduction) need to be taken into account.

The interaction between co-existing species that has had the most attention from the literature is competition (Gribben et al., 2019). Amongst competitive interactions, exploitative competition is defined as a reduction in resource availability without direct interaction between the competitors (Kim and Lasker, 1997). Exploitative competition for food could be possible between sessile species forming VMEs that are dependent on water flow to deliver food particles (Davies et al., 2008: Roberts, 2009) if the resources are limiting (Gause, 1934).

Chapter 3 consequently explored possible competition for food resources between *V. flagellum* and *D. meteor* under two different flow regimes. *Dentomuricea meteor* showed higher food incorporation under both flows speeds, but both species fed more efficiently under high flows. Flow did not affect competition interactions for food between the two tested species. Taking into consideration food incorporation, *D. meteor* could outcompete *V. flagellum*, but before assessing competition, other factors should be taken into account such as, morphology, polyp size, metabolic rate, and life histories. The different characteristics of the two octocorals give them the ability to exploit different temporal niches (different conditions present in the environment due to its variability) that might be present in their habitat (Carmo et al., 2013; Santos et al., 2013; Webb et al., 2002). For example, different polyp size allows them to feed on different prey size that are available at different times of the year. The branching structures of *D. meteor* could enable it to feed more efficiently when episodic high flows occur, while the whip shape of *V. flagellum* could enable it to feed when episodes of low flow occur. *Viminella flagellum* rises higher up in the water

column, giving it access to different prey items compared to *D. meteor*. Equally, different life histories (i.e. metabolic rate, reproductive output) in the two octocorals determine the food intake needs for different species (Boggs, 1992), *D. meteor* has a higher metabolic rate than *V. flagellum* (Rakka et al., in preparation) which would explain it being more efficient at feeding. Generally, little information is available in the life history and metabolism of deep-water octocorals. The fact that *D. meteor* and *V. flagellum* co-exist and form stable coral gardens, prompts the investigation of other possible interactions. Interactions between the species could be facilitation interactions (Gribben et al., 2019), meaning that one species facilitates for another by modifying abiotic conditions. In the case of *V. flagellum* and *D. meteor*, *D. meteor* can reduce the water flow due to its branching morphology, hence making conditions more favourable to *V. flagellum*. Better understanding of these interactions could aid with the management and designation of VMEs. For example, Pham et al. (2014) found that *D. meteor* was more sensitive to fishing efforts by longline than V. *flagellum*, if *D. meteor* is affected more, it could have implication for the facilitating interactions between the two species suggested in Chapter 3.

Competition for food resources has mainly been tested with laboratory-reared food and with food at concentrations higher than in the natural environment. Giving the same type of food to different species negates the possibility of testing species preferences for different fraction of the natural seston , and how their traits facilitate for the consumption of different particles sizes and types.

Chapter 4 explored the preference of food particle type under different flow conditions and food concentrations of co-occurring species in VMEs. The tested species (*L. pertusa, A. excavata, G. barretti, P. ventilabrum, Stryphnus sp.*) presented two different feeding strategies. *Lophelia pertusa* and *A. excavata* had higher CRs than the sponges. The results suggested that *L. pertusa* and *A. excavata* are opportunistic feeders, while sponges were more selective. Given the high variability in the trends observed, no conclusions could be drawn regarding the exploitation of different flows by active suspension feeders (*A. excavata, G. barretti, P. ventilabrum, Stryphnus* sp.) and passive suspension feeder (*L. pertusa*), but the apparent trends suggest that active suspension feeders are more efficient at higher speeds than passive suspension feeders. These results are at odds with data by Murillo et al. (2020) who found increased numbers of passive suspension feeders at maximum bottom current, but the numbers of active suspension feeders decreased. The possible contradiction between Murillo et al. (2020) and the presented results may be due to how aggregations can modulate flow, meaning flow experienced by the individuals is different from the flow measured on top of the ecosystems (Flash et al., 1998; Mienis et al., 2019).

The perceived preference of species having distinct feeding strategies for contrasting flow regimes, could suggest that the taxa can exploit different temporal niches represented by flow variability. Different flows can also enable capturing of different prey items as showed for *L. pertusa* (Chapter 4, De Clippele et al., 2018; Orejas et al., 2016). More selective species could be outcompeted when found co-occurring with opportunistic species. More detailed characterisation of food items

and the temporal variability of their availability therefore needs to be done to better assess niche partitioning. Future work should characterise DOM which provides important nutritional input to marine invertebrates, notably sponges (De Goeij et al. 2008). The results of this study suggest that the different co-occurring species partition food resources. Taking into consideration these results and research evidencing resources recycling by deep-sea fauna (de Goeij et al., 2008; 2009; 2013; Maier et al., 2020; Rix et al., 2016) it could be suggested that co-occurring species enhance each other.

5.1. Conclusions, Future directions.

Different traits from skeletal composition (e.g. sclerite shape and size, morphology) and feeding mode enable different VME indicator species to withstand the abiotic conditions, and exploit the different temporal and spatial niches that characterise the environments where they occur. As seen in Chapter 2, stiffness of the skeleton inferred from calcitic content and double head type sclerites, seem to be more suitable to tackle low to moderate flow, while skeleton flexibility is hypothesised to be more suitable under high flow conditions. In a changing ocean where ocean currents are predicted to weaken (Caesar et al., 2018; Collins et al., 2019; Frajka-Williams et al., 2019; Holt et al., 2018; Thornalley et al., 2018; Schmittner et al., 2008) traits more adapted to slow flow such as a stiffer skeleton and smaller sclerites could be advantageous. Trait differences represent strategies that can give advantages to one species over others when exploiting a given resource under specific conditions, which could translate in exploitative competition for a given resource. When tested for competition in

Chapter 3, *D. meteor* was more efficient at feeding than *V. flagellum*, with significant competition observed under high flow conditions. The different traits observed between the two species could have given *D. meteor* the advantage to capture the lab reared food provided under those specific flow conditions.

Food available in the water column is more heterogeneous and variable than lab reared food items, differences in polyp size, feeding apparatus, and feeding strategy make the different species better suited to feed on distinct fractions of the seston, as trends suggest in Chapter 4 *for L. pertusa A. excavata, G. barretti, P. ventilabrum, Stryphnus* sp. This underlines the importance of characterising the resources available and their variability, both natural and anthropogenically induced. Food changes due to climate change may represent a shift in the composition of the resource and a reduction of it. This could hamper the ability of coexisting species to partition resources. Food will become a limiting resource enabling exclusive competition.

Traits such as morphology and skeletal composition can also modify abiotic conditions. The modified conditions could be more tolerable for co-occurring species, enabling them to subsist, creating facilitating interactions, as suggested in Chapter 3. Other feedback loops can also enable species co-existence and partitioning of food resources.

Nutrient cycling is a main ecosystem function; the interactions of the different species can alter the dynamics of the ecosystems, hence they should be also taken into account. It is difficult to draw conclusions on how nutrient cycling

processes could be affected if one species is outcompeted due to flow and food availability changes. For example, sponges feed preferentially on bacterioplankton, corals and bivalves feed preferentially on bigger food particles. If sponges were to be outcompeted, bacteria populations could grow uncontrolled and create hypoxic conditions. Maier et al. (2020) evidenced the usage of *A. e*xcavata pseudofeces by ophiurouids, if *A. excavata* were to be outcompeted, it could have repercussions for the wider ecosystem. Species might also be dependent on one another to access food items. For example, flow modification by *D. meteor* might enable *V. flagellum* by reducing the speed of the impinging flow and creating eddies. The creation of eddies could facilitate food aquisitioon for *V. flagellum*. This was evidenced in Chapter 3, where trends suggested that *V. flagellum* was more efficient at exploiting food resources when it was in competition conditions. Cardinale et al. (2006) suggested that the general effect of decreasing species richness is a decrease in biomass abundance, leading to less complete depletion of resources, consequently less nutrient fixation.

In order to better understand species interactions and their relation to the environment and how will they react to changing conditions, multiple traits need to be investigated (Kraft et al., 2015b). Equally, the life history of the species forming VMEs should be taken into consideration to assess their metabolic needs, and if the metabolic needs are met by the available food resources. Species having a lower metabolic rate would not need as much food as species having a higher one, and thus merely assessing feeding efficiency might not be sufficient to understand competition. As highlighted in this thesis, species interactions are

broader than competition. The different interactions should be studied because they can control population dynamics along environmental gradients and affect rates of species range shifts, contributing to understanding and predicting the dynamics of populations and communities at smaller spatial scales (Lavergne et al., 2010).

Vulnerable marine ecosystems designation is a management tool that manages these ecosystems against fishing pressure. This tool can offer protection against other exploitative activities, but the harmful effects of exploitative industries, as summarised in Chapter 1, can be exacerbated by the cumulative effects of climate change that hampers their recovery and preservation. Recently the scientific community has acknowledged how climate change should be take into consideration when planning management strategies. Levin et al., (2020) proposed several tools to integrate climate change predictions and management, amongst them species distribution models can help identify refugia were the different ecosystems will not be as affected by changing conditions. The identified refugia could be of major importance to support the recovery of damaged ecosystems. Current closed areas to preserve VMEs and other managed areas are based in present environmental conditions (Johnson et al., 2018). Nevertheless, areas closed to protect VMEs are predicted to be impacted by climatic change, which will reduce their efficiency in protecting the ecosystems (Johnson et al., 2018). Predicting climate refugia for the 7 studied species can be a daunting task. Morato et al. (2020) predicted the climate-induced changes in the suitable habitat of CWC, and found very limited possible refugia for *L. pertusa* and octocorals. To

my knowledge, no such modelling has been done for sponges or *A. excavata*. Nevertheless, species having a broader geographical range have better chances of surviving extinction events (Orzechowski et al., 2015), thus *L. pertusa, G. barretti, Stryphnus* sp, and *P. ventilabrum* having more extensive ranges should have better probabilities of surviving than *V. flagellum* and *D. meteor*. Equally, *V. flagellum* should have better possibilities of survival than *D. meteor* given their different depth ranges and the fact that *V. flagellum* is also found in the Mediterranean Sea (Giusti et al., 2012). *Dentomuricea meteor* is more sensitive than *V. flagellum* to the effects of ocean acidification, most likely due to its higher metabolism (Rakka, et al., in preparation). Given the projected decrease in available food reaching the deep sea, it could be possible that *D.meteor* will struggle meeting its metabolic needs.

Species distribution models (SDMs) are a recent tool to understand the distribution of species and how it can change under climate change (Morato et al., 2020); they are powerful instruments to help in management decisions. Currently, SDMs rarely take into account biotic interactions (Lavergne et al., 2010). Including biotic interactions in such models can give more realistic projection of the future of the ecosystems. Understanding that *V. flagellum* might benefit from the presence of *D. meteor* in high flow environments, and that sponges can process DOM to make it more available to other species, can be crucial knowledge when crafting SDMs. Gathering robust data on species interactions requires lab experiments, *in situ* observation, and *in situ* experimental approaches (landers, Free Ocean CO_2 Enrichment). Landers could monitor the behaviour of the co-

occurring species while recording environmental variability, which would help elucidated seasonal niche partitioning. *In situ* pulse feeding experiments with isotopically labelled food could also be performed and filmed to monitor species behaviour and food utilisation. Free Ocean CO_2 enrichment experiments could be useful to monitor the interactions of the different co-occurring species under changing conditions. These processes can prove difficult since deep-sea exploration endeavours are effort and time consuming, also acquiring enough replicates for laboratory experiments is challenging.

Environmental variability can modulate the interactions of co-occurring species, but so far, models incorporate long term, and global scale changes in abiotic conditions, but ocean weather, meaning small scale variation, is seldom taken into account (Bates et al., 2018). Small regional changes in flow regimes can favour different species depending on the traits they possess affecting their interactions, which can alter ecosystem dynamics. In order to better predict how VME indicator taxa will respond to anthropogenic forcing, small scale variations should be taken into account to avoid wrong prediction for the specific systems studied (Bates et al., 2018). The challenge again relies on the difficulty of obtaining such data for deep-sea environments, but with new technology such as ocean observatories it could be possible (e.g. Osterloff et al., 2019).

Future research should be aimed to properly understand species interactions in order to understand ecosystem functioning. Better characterising the phylogeny of co-occurring species is also a future avenue of research, using

species traits, their phylogenetic relationships, and abiotic factors can help to disentangle the mechanisms underlying community assembly (Murillo et al., 2020; Quattrini et al., 2017). In this thesis, I found preliminary evidence that skeleton composition of octocorals can confer advantages to survive and feed under different flow regimes as seen in Chapter 2. Equally, morphology can modulate flow and enables feeding under different conditions as discussed in Chapter 3. Active and passive suspension feeder traits could give advantages when feeding under different flow regimes, and the different species create recycling pathways minimising competition as evidenced in Chapter 4, but in order to better understand the distinction, more in depth investigation on the intricate differences between active and suspension feeders are needed. Functions of the traits have to be better related to the environment. Studying phenotypical variations occurring in separate populations existing under different conditions will help us to quantify the level of variation due to differences in environmental variables. *In situ* observation of population assemblages with proper characterisation of the traits and environmental variability will help couple traits and functions. Subsequent lab experiments could help to further isolate traits and their functions. This thesis sheds light into the importance of understanding how species interactions and the different traits could shape the responses of VME indicator taxa to changing conditions such as flow and food avaliability.

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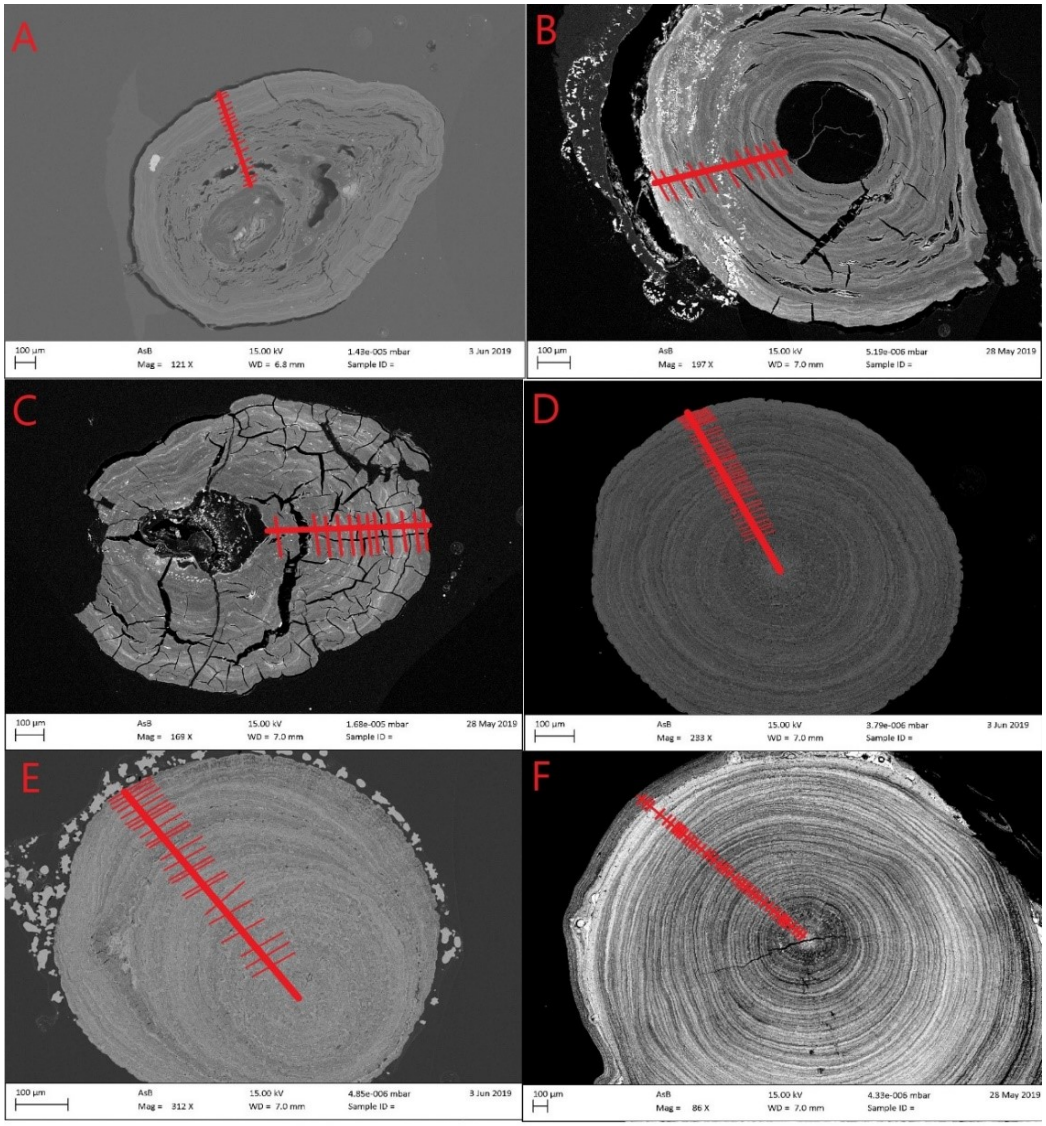
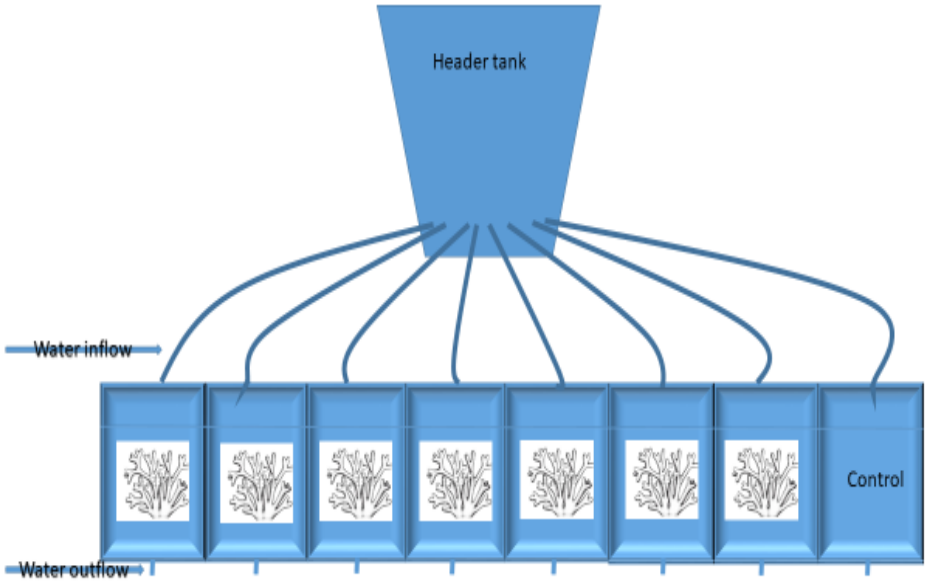
Supplementary material

Supplementary material 2.1



Cross-Sections used for sclerochronology, The individual diagonal red lne is and arbitrary assessment to measure the distance from the skeleton core to the edge. Each small "horizontal red line represents a counted ring. (A):*D. meteor* 15 growth rings and a diameter of 1.3 mm. Calculated radial growth of 0.08 mm year^{-1} (B): *D. meteor* 11 growth rings and a diameter of 1 mm calculated radial growth rate 0.1 mm year^{-1}. (C): *D.meteor* 12 growth rings and a diameter of 1.2 mm., calculated radial growth rate 0.01 mm year^{-1}. (D):*V. flagellum* 37 growth rings and a diameter of 0.9 mm, calculated radial growth rate 0.025 mm year^{-1} (E): *V. flagellum*, 23 growth rings and a diameter of 0.75 mm, calculated radial growth rate 0.033 mm year $^{-1}$. (F): *V. flagellum*, 44 rings and a diameter of 3.4 mm, calculated radial growth 0.077 mm year^{--1}.Note the cracks present in the *D. meteor* cross sections are due to sample processing.

Supplementary material 4.1



Schematic view of experimental chambers used in Chapter 4. Each experimental chamber internal dimensions (w*l*h) were: 10.5 * 22 * 10 cm. Chambers were design to minimise water recirculation (Strohmeier et al., 2009)

Supplementary material 4.2

Mean Particulate Organic Matter (POM) mg l^{-1} and Suspended Particulate Matter (SPM) mg l^{-1} given to the organisms per species and food treatment± SD mg l^{-1}.

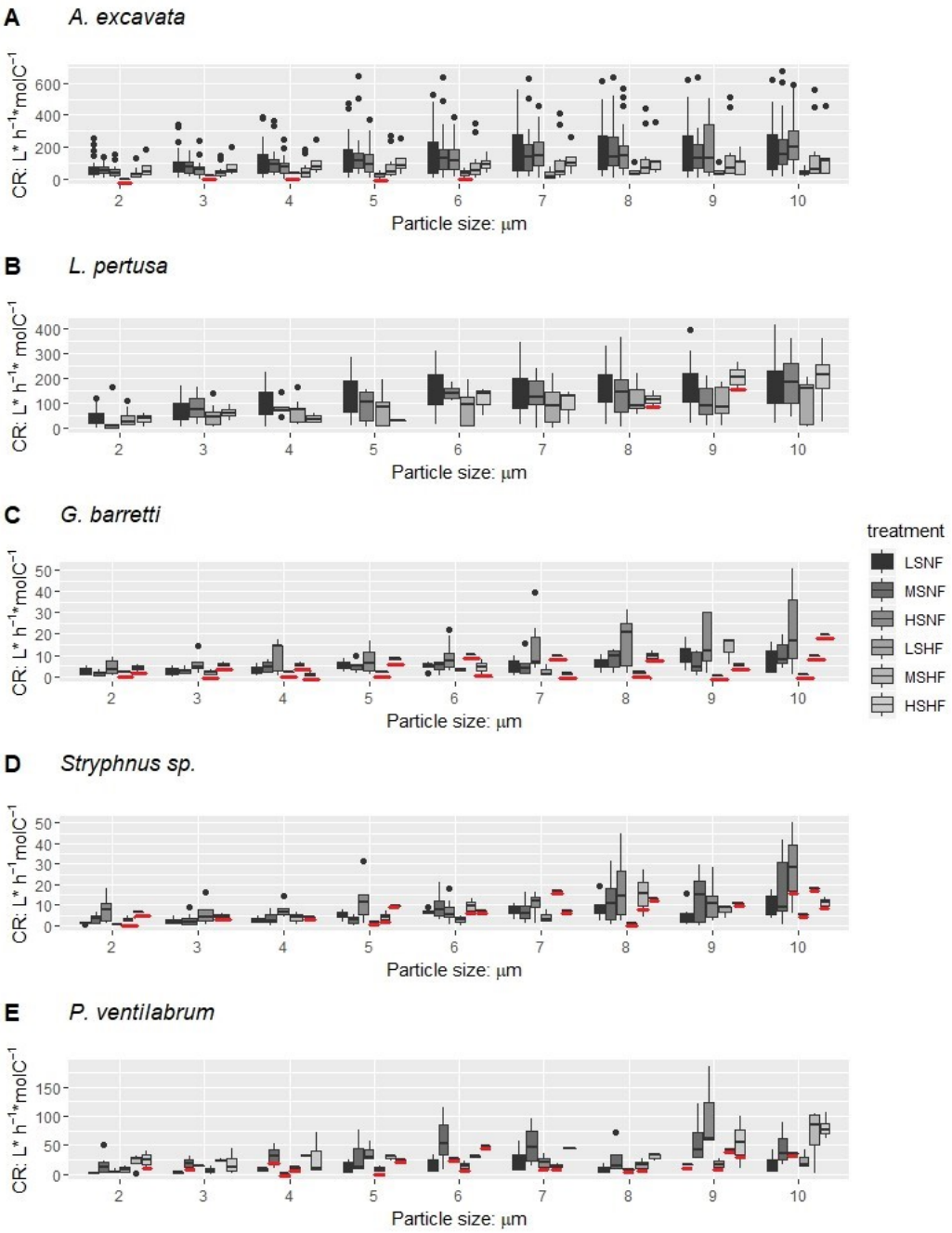
		A. excavata	*L. pertusa*	*G.barretti*	*Stryphnus sp.*	*P. ventilabrum*
Normal Food	SPM mg l^{-1}	0.14 ± 0.04	0.11 ± 0.05	0.09 ± 0.01	0.08 ± 0.00	0.08 ± 0.01
	POM mg l^{-1}	0.04 ± 0.02	0.03 ± 0.02	0.02 ± 0.00	0.03 ± 0.01	0.02 ± 0.01
High Food	SPM mg l^{-1}	0.18 ± 0.03	0.23 ± 0.18	0.11 ± 0.02	0.11 ± 0.02	0.14 ± 0.06
	POM mg l^{-1}	0.06 ± 0.03	0.08 ± 0.07	0.03 ± 0.01	0.04 ± 0.01	0.04 ± 0.01

Supplementary material 4.3

Table showing percentage of positive Clearance Rates per species and per treatment calculated using the PAMAS results.

	A. excavata	*L. pertusa*	*G. barretti*	*Stryphnus. sp*	*P. ventilabrum*
Low Speed Normal Food	89.29	95.24	57.14	28.57	42.86
Medium Speed Normal Food	77.78	35.71	50.00	50.00	42.86
High Speed Normal Food	82.14	NA	42.86	42.86	28.57
Low Speed High Food	28.57	57.14	14.29	NA	28.57
Medium Speed High Food	78.57	57.14	28.57	28.57	42.86
High Speed High Food	57.14	NA	NA	14.29	28.57

Supplementary material 4.4



Boxplots of the calculated Clearance Rates (CRs) for each species under each treatment and particle size. Red bars under the box plots indicate the data set contained less than 3 data points. Black dots indicate outliers. (A): Boxplot showing CRs for *A. excavata* for each particle under each treatment. (B): Boxplot showing CRs for *L. pertusa* for each particle under each treatment. (C): Boxplot showing CRs for *G.barretti* for each particle under each treatment. Note that boxplots for the treatment HSHF and particle sizes 2, 3, 5 and 8 µm are not shown because there was no data points. (D): Boxplot showing CRNs for *Stryphnus* sp. for each particle under each treatments. Note that boxplots for treatments LSHF and particle sizes 3 and 4 µm and treatment HSHF, particle sizes 3 and 9 µum are not shown because of absence of data points. (E): Boxplot showing CRs *for P. ventilabrum* for each particle under each treatments. Note that that box plot for treatment HSHF and particle sizes 8 and 9 µm are not shown because of data points absence. . For each treatment combination. LS: low flow speed; MS: medium flow speed; HS: high flow speed; NF: normal food quantity; HF: high food quantity

Supplementary material 4.5

Table showing p-values of statistical significant results of analysis including particle size. . For each treatment combination. LS: low flow speed; MS: medium flow speed; HS: high flow speed; NF: normal food quantity; HF: high food quantity

Treatments and p-values								
	LSNF		MSNF		HSNF		LSHF	
Species	Particle size µm	p-value	Particle size µm	p-value	Particle size µm	p-value	Particle size µm	p-value
	2-6	0.00042					2-8	0.0185
A.excavata	2-7	0.0176					2-9	0.0154
	2-8	0.00028					2-10	0.0248
	2-9	0.00146						
	2-10	0.0001						
	3-8	0.0435						
	3-10	0.021						
	4-10	0.00095						
L.pertusa	2-5	0.006	2-4	0.0462				
	2-6	0.0004	2-6	0.0054				
	2-7	0.0004	2-7	0.0193				
	2-8	0.0002	2-8	0.0396				
	2-9	0.0001	2-9	0.0111				
	2-10	0.0001	2-10	0.0001				
G. barretti	3-9	0.0181	2-8	0.0078				
			2-9	0.0459				
			2-10	0.0001				
P. ventilabrum					2-9	0.0258		

Supplementary material 4.6

Table of showing percentage of positive Clearance rates results from the Flow cytometry analyses for silt,algae bacteria under the different experimental conditions for each species For each treatment combination. LS: low flow speed; MS: medium flow speed; HS: high flow speed; NF: normal food quantity; HF: high food quantity.

	Particle type	***A.excavata***	***L.pertusa***	***G.barretti***	***Stryphnus .sp.***	***P.ventilabrum***
LSNF	Silt	60.71	19.05	57.14	78.57	28.57
	Algae	92.86	38.10	85.71	64.29	57.14
	Bacteria	50.00	23.81	78.57	92.86	85.71
MSNF	Silt	25.93	35.71	71.43	57.14	85.71
	Algae	55.56	85.71	78.57	100.00	85.71
	Bacteria	55.56	92.86	71.43	85.71	85.71
HSNF	Silt	67.86	NA	85.71	57.14	85.71
	Algae	78.57	NA	85.71	71.43	42.86
	Bacteria	78.57	NA	42.86	92.86	85.71
LSHF	Silt	14.29	57.14	28.57	71.43	100.00
	Algae	42.86	92.86	57.14	100.00	100.00
	Bacteria	57.14	50.00	100.00	85.71	100.00
MSHF	Silt	57.14	14.29	14.29	42.86	57.14
	Algae	71.43	14.29	NA	28.57	57.14
	Bacteria	64.29	28.57	85.71	57.14	100.00
HSHF	Silt	71.43	NA	100.00	14.29	57.14
	Algae	42.86	NA	NA	42.86	85.71
	Bacteria	42.86	NA	85.71	71.43	57.14